UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFETS DE L'ENNEIGEMENT ET DE L'ENTOURBEMENT SUR LA PHYSIOLOGIE DE L'ÉPINETTE NOIRE ET DU PEUPLIER FAUX-TREMBLE EN FORÊT BORÉALE QUÉBÉCOISE

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN SCIENCES DE L'ENVIRONNEMENT

PAR

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MAI 2010

UNIVERSITÉ DU QUÉBEC À MONTRÉAL
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Avant-propos

Ce mémoire présente les résultats d'une étude réalisée dans le cadre de ma maîtrise en sciences de l'environnement. La première section du rapport introduit le sujet par une mise en contexte et une revue de la littérature actuelle. Le corps du texte, rédigé en anglais, a été écrit sous la forme d'un article scientifique intitulé : «Root zone temperature in boreal spring depends on thermal insulation and controls photosynthetic capacity in *Picea mariana* and *Populus tremuloides* ». L'article sera soumis pour publication à l'été 2010. Une conclusion générale suit l'article, réunit les principaux résultats de l'étude et fait le lien avec les objectifs de recherche mentionnés en introduction.

Ce projet a initialement été élaboré par Yves Bergeron, Frank Berninger et le regretté Bernhard Denneler. Ce sont eux qui ont conçu et implanté le dispositif expérimental. J'ai moi-même collecté et compilé les données. Les analyses d'isotopes stables ont été réalisées dans les laboratoires d'Ingo Ensminger de l'Institut de recherche forestière Baden-Württemberg et d'Arthur Gessler du Centre de Biologie des Systèmes de Fribourg, en Allemagne. Les analyses statistiques ont été réalisées à l'UQÀM avec l'aide précieuse de Stéphane Daigle. Frank Berninger, Ingo Ensminger et Yves Bergeron ont tous joué un rôle important dans l'interprétation des résultats.

Remerciements

Au terme de ce travail, je tiens d'abord à remercier mon directeur de recherche, Frank Berninger, pour sa disponibilité et sa patience, ainsi que mon co-directeur Yves Bergeron, pour son soutien et sa confiance. Merci à Ingo Ensminger et Arthur Gessler, pour m'avoir accueillie dans leurs laboratoires, pour l'aide technique, les discussions stimulantes et les bons conseils. Merci à Dan Kneeshaw et Igor Drobyshev pour leurs commentaires sur le texte.

Merci à ceux qui m'ont assistée sur le terrain et qui ont contribué à rendre cet été à la Baie-James tellement agréable : Raymond Lanctôt, Kasia Richer-Juraszek et Marie-Noëlle Caron. Merci à Mélanie Desrochers, Luc Lauzon, Stéphane Daigle et aux autres professionnels du CEF qui nous facilitent tellement la tâche dans nos projets. À mes collègues étudiants-chercheurs du CEF : Aurélie Terrier, Albanie Leduc, Guillaume Sainte-Marie, Maryse Marchand et Dave Gervais, merci pour votre présence quotidienne, le support moral, et les bons moments partagés!

Finalement, un merci particulier à mes proches pour leur présence et leurs encouragements constants : Nicole, Isabelle, Catherine, Myriam, Martin et Alex.

Cette recherche a été rendue possible grâce au financement du Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), de la Chaire CRSNG-UQAT-UQÀM en aménagement forestier durable et d'Ouranos.

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C	Carbone
CO_2	Dioxyde de carbone
ETR	Taux de transport d'électrons ($\mu mol\ m^{-2}s^{-1}$)
ETR_{max}	Taux maximal de transport d'électrons ($\mu mol\ m^{-2}s^{-1}$)
F_m	Rendement quantique maximal d'une feuille adaptée à la noirceur
F_o	Rendement quantique minimal d'une feuille adaptée à la noirceur
F_v	Rendement quantique variable d'une feuille adaptée à la noirceur (F_m - F_o)
F_v/F_m	Rendement quantique potentiel du PSII
N	Azote
P	Phosphore
PPFD	Densité photosynthétique du flux de photons ($\mu mol\ m^{-2}$)
$PPFD_{sat}$	Densité photosynthétique du flux de photons à saturation ($\mu mol\ m^{-2}$)
PSI et PSII	Photosystèmes I et II
$\Delta F/F_m$	Rendement quantique du PSII
$\Delta F/F_{m\ sat}$	Rendement quantique du PSII sous lumière saturante
$\Delta^{13}C$	Mesure du ratio d'isotopes stables ^{13}C:^{12}C (‰)
$\Delta^{15}N$	Mesure du ratio d'isotopes stables ^{15}N:^{14}N (‰)
$\Delta^{18}O$	Mesure du ratio d'isotopes stables ^{18}O:^{16}O (‰)

RÉSUMÉ

En forêt boréale, les couverts de mousses et de neige, deux isolants et importants régulateurs de la température du sol, sont susceptibles de changer considérablement avec les changements climatiques prévus. Nous avons évalué la réponse physiologique de l'épinette noire et du peuplier faux-tremble à différentes épaisseurs de mousses et de neige dans la pessière à mousses du sud-ouest du Québec. Pendant un an, des épinettes et peupliers de 10 ans ont poussé avec un couvert additionnel de mousses, sans couvert de mousses, avec un couvert de neige modifié pour retarder ou accélérer le dégel du sol, ou avec une dose de fertilisant d'azote. Au cours de la saison de croissance 2008, nous avons suivi le débourrement des deux espèces, leur rendement de fluorescence chlorophyllienne et leur contenu foliaire en carbone, azote et en isotopes stables ^{13}C, ^{15}N et ^{18}O. Au printemps, les traitements qui ont impliqué l'ajout d'une couche isolante de mousse ou de neige ont refroidi le sol, tandis que l'enlèvement de la mousse et de la neige l'ont réchauffé. Une tendance prédominante est que le couvert du sol, qu'il soit neigeux ou végétal, a accru le taux de reprise de la photosynthèse au printemps. Réciproquement, l'enlèvement du couvert de neige et de mousses a été néfaste pour la reprise de la photosynthèse, particulièrement chez l'épinette, où l'on a enregistré un taux de transport d'électrons maximal 39.5% plus bas sans mousses qu'avec mousse additionnelle, et 16.3% plus bas suivant un dégel accéléré qu'avec un dégel retardé. Le rendement potentiel du PSII (F_v/F_m) était 3.3% plus bas sans mousse qu'avec mousse additionnelle, et 3.8% plus bas avec un dégel accéléré qu'avec un dégel retardé. Ces taux de reprise modérés étaient généralement accompagnés de contenus foliaires en azote plus bas. La reprise de photosynthèse et l'assimilation de nutriments affaiblis en l'absence d'une couche isolante de mousses ou de neige ont été principalement attribuées à une assimilation réduite de nutriments occasionnée par des changements au niveau de la microbiologie du sol probablement causés par une plus grande amplitude des variations journalières de la température du sol. Il est probable que les champignons mycorhiziens et/ou organismes décomposeurs du sol en aient été affectés dans leurs fonctions, perturbant les dynamiques de N du sol. Les deux espèces ont été affectées dans le même sens, mais le peuplier a réagi de façon moins importante. Le système racinaire de l'épinette, qui se développe en surface dans le profil du sol, rend l'assimilation de nutriments par voie mycorhizienne plus susceptible aux variations de température de l'air que le peuplier, qui développe ses racines davantage en profondeur.

Mots clés : *Picea mariana*, *Populus tremuloides*, changements climatiques, couvert de neige, couvert de mousses, température du sol, photosynthèse, fluorescence chlorophyllienne, rendement quantique du PSII, taux du transport d'électrons, isotopes stables.

INTRODUCTION GÉNÉRALE

Problématique

Selon le quatrième rapport du Groupe intergouvernemental d'experts sur l'évolution du climat (GIEC), la température globale de l'atmosphère a connu une hausse de 0.7ºC au cours du 20e siècle, et une augmentation supplémentaire de 1.8 à 4.0ºC est prévue d'ici 2090 (Christensen et al. 2007). Ce réchauffement est plus prononcé aux latitudes élevées, et le sud-ouest du Québec a été particulièrement touché avec une augmentation de 0.8 à 1.3ºC durant la période 1960-2003 (MRNF 2004). Au cours du prochain siècle, cette tendance pourrait se poursuivre avec un réchauffement pouvant s'élever jusqu'à 7.0ºC en hiver (Christensen et al. 2007). Ce réchauffement pourrait être accompagné d'une hausse de précipitations de 10 à 25% par rapport aux conditions actuelles (Christensen et al. 2007). En forêt boréale, les couverts de mousses et de neige, deux isolants et importants régulateurs de la température du sol, sont susceptibles de changer considérablement avec les changements climatiques prévus (Campbell et al. 2005; Saxe et al. 2001).

Sur la ceinture d'argile du Québec et de l'Ontario, de larges étendues de forêt sont prônes à l'accumulation de matière organique et colonisées par des bryophytes qui contribuent à l'élévation de la nappe phréatique (Fenton et al. 2005; Longton 1992). Selon de récentes simulations climatiques, l'augmentation prévue de précipitations sera insuffisante pour compenser l'accroissement de l'évapotranspiration en été, ce qui pourrait créer des conditions plus sèches qu'à présent (Girardin and Mudelsee 2008). Ces nouvelles conditions auraient le potentiel d'abaisser la nappe phréatique et d'accélérer la décomposition de la matière organique du sol (Saxe et al. 2001), y réduisant l'accumulation de mousses. Réciproquement, des précipitations accrues pourraient avoir l'effet contraire, et amplifier la colonisation de mousses. L'effet des changements climatiques sur le couvert de mousses est difficile à prévoir et dépendra de la balance entre les effets de la température et des précipitations.

Le couvert neigeux variera également avec les changements climatiques, avec comme conséquence directe une fonte des neiges plus hâtive au printemps, et

l'établissement d'un couvert neigeux plus tard à l'automne (Brown and Mote 2009; Christensen et al. 2007), exposant le sol aux variations de la température de l'air plus longtemps en automne et au printemps.

La température du sol joue un rôle déterminant dans l'activité physiologique des arbres, leur croissance et leur distribution (Bowen 1991). Celle-ci influence directement l'absorption de l'eau et des nutriments, le taux de décomposition de la matière organique, et indirectement la disponibilité des nutriments (Kozlowski et al. 1991; Kramer 1983). Au printemps, la température du sol détermine, avec la photopériode et la température de l'air, le moment et le taux de reprise des processus physiologiques comme le débourrement et la photosynthèse (Ensminger et al. 2004), et ultimement, le taux de croissance des arbres. La productivité forestière est un enjeu important au Québec, puisqu'elle est à la source d'un des principaux moteurs économiques de la province. On estime, en effet, que près de 80 000 emplois sont générés par l'industrie forestière (MRNF 2007), qui est directement dépendante de la disponibilité de la matière ligneuse. Afin de mitiger l'impact négatif qu'auront les changements climatiques à long terme sur la forêt boréale québécoise, il est nécessaire de prévoir leurs effets sur l'écosystème forestier. Nous proposons donc d'évaluer la réponse physiologique de deux espèces parmi les plus importantes en forêt boréale québécoise, l'épinette noire (*Picea mariana* (Mill.) B.S.P.) et le peuplier faux-tremble (*Populus tremuloides* Michx.) à différentes épaisseurs de mousse et de neige. L'épinette noire est reconnue pour sa capacité à croître en sols froids et faiblement drainés (Burns and Honkala 1990a), ayant une capacité photosynthétique plus sensible aux température de sol élevées que le peuplier faux-tremble (Dang and Cheng 2004), qui croit typiquement en sols plus chauds et mieux drainés (Burns and Honkala 1990b).

État des connaissances

Effets du couvert de mousses sur les conditions du sol

Les qualités isolantes de la mousse en font un important régulateur de la température du sol en forêt. La mousse crée une barrière physique qui fait obstacle aux rayons du soleil, en plus d'absorber une partie de cette énergie pour sa photosynthèse

(Gornall et al. 2007). De plus, les espaces d'air entre les tiges de mousses rendent la conductivité thermique des tapis de mousses plus basse que celle du sol (Beringer et al. 2001). Une épaisse couche de mousse refroidit donc le sol pendant la saison de croissance, et réduit l'amplitude des variations journalières de température avant l'établissement d'un couvert neigeux à l'automne, et après la fonte des neiges au printemps (Gornall et al. 2007). En manipulant l'épaisseur du couvert de mousses dans la toundra arctique, Gornall *et al.* (2007) ont mesuré que le sol était plus chaud de 1ºC sous un matelas de mousse de 3 cm d'épaisseur que sous un matelas de 6 cm. La même étude a démontré qu'un couvert de mousse plus épais pouvait retarder le dégel du sol de plusieurs semaines au printemps. L'enlèvement du couvert de mousses au sol d'une pessière noire d'Alaska a significativement abaissé le niveau du permafrost, approfondissant la couche active de plus d'un mètre (Dyrness 1982).

Les mousses sont également reconnues pour leur capacité à modifier le régime hydrologique du sol. La colonisation de sphaignes en forêt boréale entraîne une augmentation de la capacité de rétention d'eau du sol, élevant le niveau de la nappe phréatique (Longton 1992). Un épais couvert de mousses restreint l'évapotranspiration, aidant à la rétention d'humidité dans le sol (Zimov et al. 1995). La température du sol en est davantage réduite, et ces conditions froides et anaérobiques ralentissent l'activité biologique du sol (Longton 1992; Oechel and Van Cleve 1986). En pessière à mousses, le faible taux de décomposition de la matière organique, couplé à la production d'une litière de faible qualité, contribuent à l'accumulation d'une couche épaisse de matière organique faiblement décomposée au sol. Les nutriments, emprisonnés dans l'horizon supérieur du sol, demeurent indisponibles pour l'assimilation par les arbres (Longton 1992; Oechel and Van Cleve 1986). En sol paludifié, le taux de croissance des arbres est réduit (Van Cleve and Viereck 1981) et l'établissement des semis est inhibée (Bonan and Shugart 1989). Sur la ceinture d'argile du Québec et de l'Ontario, cette accumulation graduelle de matière organique au sol, aussi appelée paludification, est responsable de la transition de forêts productives en tourbières (Crawford et al. 2003).

Les mousses modifient également la dynamique nutritionnelle du sol forestier en interceptant les nutriments atterrissant au sol de la canopée ou par précipitations. Ces nutriments sont emmagasinés dans les tapis de mousses plutôt que d'être lessivés vers les horizons plus profonds du sol, hors du système (Oechel and Van Cleve 1986). En plus de leur rôle de réservoir de nutriments, les mousses sont vues comme une source importante de N au sein des écosystèmes forestiers. La fixation biologique de N atmosphérique est la source première de ce nutriment en forêt boréale (Cleveland et al. 1999), et cette fixation serait accomplie principalement par des cyanobactéries qui colonisent les matelas de mousses dominés par *Pleurozium schreberi* (DeLuca et al. 2007; 2002). La fixation de N_2 varie grandement dans le temps et l'espace, avec un taux annuel de 0.5 kg N ha^{-1} en début de succession à 2 kg N ha^{-1} en forêt mature (Zackrisson et al. 2004). Sur une base annuelle, DeLuca *et al.* (2002) ont suggéré que le taux de fixation de N_2 atteignait un sommet en septembre et était maintenu jusqu'en novembre. En forêt boréale, l'épinette noire et le peuplier faux-tremble s'associent avec des champignons ectomycorhiziens (Doucet and Côté 2009) qui croissent immédiatement sous la couche de mousses (Carleton and Read 1991) et qui développent d'extensifs réseaux mycéliens reliant les racines des arbres au tapis de mousses sus-jacent. Certains auteurs ont suggéré que le N fixé ainsi que les autres nutriments emprisonnés dans les tapis de mousses pouvaient être transférés par voie mycorhizienne jusqu'à la rhizosphère des arbres (Carleton and Read 1991; Chapin III et al. 1987). Par exemple, Carleton et Read (1991) ont observé des transferts de nutriments par voie mycorhizienne à partir de tapis de *Pleurozum schreberi* jusqu'aux racines du pin tordu (*Pinus contorta* Douglas), et Chapin et al. (1987) ont rapporté des observations similaires pour l'épinette noire. Une façon d'estimer la proportion de N assimilé par voie mycorhizienne est la mesure du contenu foliaire en isotopes stables ^{15}N. En transférant des composés organiques d'azote aux racines des arbres, les champignons mycorhiziens discriminent contre le ^{15}N, et épuisent leur hôte en ^{15}N (Hobbie et al. 2008; Hobbie et al. 2009).

Effets du couvert neigeux sur les conditions du sol

La neige est aussi un important régulateur de la température du sol en forêt boréale. Sa faible conductivité thermique et son albédo élevé en font un excellent isolant thermique. Un épais manteau neigeux en hiver maintient le sol à des températures avoisinant le point de congélation (Decker et al. 2003; Hardy et al. 2001), tandis qu'un sol dénudé de neige en hiver gèle en profondeur (Körner 2003). En forêt boréale, où une couche de neige isolante persiste pendant toute la saison hivernale, les racines des arbres ne développent qu'un endurcissement au froid minimal, étant donc généralement moins adaptées au gel que les parties aériennes de l'arbre (Auclair et al. 1996; Sakai and Larcher 1987). À l'automne, les racines développent leur endurcissement au froid plus tard que les parties aériennes (Sakai and Larcher 1987). Lors d'une année à enneigement tardif ou dans le cas d'une fonte momentanée en hiver, le gel lui-même risque d'endommager ou de tuer les racines des arbres, restreignant l'assimilation d'eau et de nutriments au cours de la saison de croissance suivante. La capacité d'un arbre à assimiler l'eau du sol peut être mesurée par l'analyse du contenu foliaire en isotopes stables ^{13}C et ^{18}O. D'abord, le signal ^{13}C des feuilles est formé pendant la photosynthèse suite à une discrimination par l'enzyme Rubisco contre le $^{13}CO_2$ (Körner 2003). En situation de stress hydrique, la conductance stomatique réduite contribue à l'expression du signal ^{13}C (Betson et al. 2007; Körner 2003). Le signal ^{18}O, quant à lui, apparaît lorsque le $H_2{}^{16}O$, qui présente une pression de vapeur plus haute que le $H_2{}^{18}O$, est évaporé hors des feuilles (Barbour and Farquhar 2000). Le signal $\delta^{18}O$ reflète les variations de conductance stomatique, alors que le $\delta^{13}C$ peut varier soit en fonction de la conductance stomatique, ou du taux de photosynthèse (Cernusak et al. 2009). L'analyse des deux paramètres peut donc renseigner sur les mécanismes responsables des variations de la capacité d'utilisation de l'eau du sol (Cernusak et al. 2009).

La température du sol contrôle la capacité des racines à absorber l'eau du sol. Le gel du sol réduit l'assimilation d'eau et de nutriments par les arbres en augmentant la viscosité de l'eau et la résistance des racines à sa circulation (Kramer 1983). En plus d'une capacité d'absorption limitée, les racines présentent un métabolisme et une croissance réduite en sol froid (Kozlowski and Pallardy 1996; Lopushinsky and Max 1990; Peng and

Dang 2003). Certaines études indiquent toutefois que de l'eau est assimilée par les racines durant l'hiver (Owston et al. 1972; Polunin 1933), mais il est généralement considéré que l'eau du sol devient indisponible à partir de -1ºC (Tranquillini 1979). Cet apport en eau est essentiel à la survie hivernale des feuilles chez les conifères (Marchand 1996), puisque la perte d'eau par évapotranspiration au cours de l'hiver peut être suffisante pour créer un stress hydrique dommageable pour les feuilles (Boyce et al. 1992; Boyce et al. 1991). Tôt au printemps, lorsque la température de l'air dépasse le point de congélation, le gradient de pression de vapeur entre les feuilles et les racines des conifères augmente. Dans un sol gelé, l'eau perdue par évapotranspiration ne peut être remplacée par les racines, et les chances d'un stress hydrique chez les feuilles augmentent (Boyce and Lucero 1999; Repo et al. 2005; Tranquillini 1982). Si un couvert neigeux est présent au sol, celui-ci est maintenu à des températures avoisinant le point de congélation, et l'assimilation d'eau par les racines est alors possible. Boyce et Lucero (1999) ont démontré que les arbres de petite taille étaient davantage dépendants de l'apport en eau du sol pendant l'hiver que les arbres de plus grande taille, qui utilisent l'eau emmagasinée dans leur tronc. Au printemps et en hiver, les conifères enfouis sous le manteau neigeux profitent de conditions plus humides qu'à l'air ambiant, et donc de déficits hygrométriques plus bas (Boyce and Lucero 1999). La température foliaire est également réduite sous la neige, et les chances de stress hydrique dû à un taux d'évapotranspiration trop élevé sont amoindries (Boyce and Lucero 1999). La neige protège également contre les effets destructeurs du vent, de la glace et des radiations solaires (Körner 2003).

L'absence de neige au sol par temps froid peut influencer ses populations microbiennes et la capacité de rétention des nutriments du sol. Il est maintenant reconnu que l'activité biologique des sols se poursuit durant l'hiver, en sols froids (0 à 5ºC) ou même gelés (Brooks et al. 1998; Clein and Schimel 1995). À l'automne et au printemps, l'absence d'accumulation de neige peut exposer le sol à des cycles de gel-dégel (Decker et al. 2003; Hardy et al. 2001) qui y causent la rupture des cellules microbiennes (Ross 1972). Chacun de ces cycles est généralement suivi par un regain d'activité respiratoire soutenu par la décomposition de la matière organique soluble dégagée par les cellules lysées (Skogland et

al. 1988). Schimel et Clein (1996) ont observé qu'un seul cycle de gel-dégel avait tué 50% d'une population microbienne, que chaque cycle était suivi par une hausse du taux de respiration, mais que ce taux diminuait après plusieurs cycles successifs. Après trois cycles, la capacité de la population à décomposer la matière organique du sol et à minéraliser le N était significativement inhibée. DeLuca *et al.* (1992) ont observé que les cycles de gel-dégel du sol étaient associés à une hausse du taux de minéralisation, et au dégagement de N minéral dans le sol. Ron Vaz *et al.* (1994) ont documenté un dégagement de P plus élevé dans un sol riche en matière organique qui avait été soumis à des cycles répétés de gel-dégel. Fitzhugh *et al.* (2001) ont enregistré un plus grand dégagement de C, N et P inorganique dans un sol privé de son couvert de neige en début d'hiver. Ces nutriments, relâchés dans la solution du sol alors que la demande en nutriments des arbres est faible, sont lessivés hors de l'écosystème et le sol en reste appauvri. Également, il a été démontré que des cycles de gel-dégel plus nombreux pouvaient modifier la structure du sol. Par exemple, Edwards (1991) a trouvé que les cycles de gel-dégel réduisaient la stabilité et la taille des agrégats du sol. En enlevant la neige d'un sol forestier au cours de deux hivers consécutifs, Tierney *et al.* (2001) ont observé des dommages aux racines fines, probablement causés par les mouvements du sol et la formation de pellicules de glace durant les épisodes de gel du sol.

Température, photosynthèse et productivité

Le domaine boréal est caractérisé par de grands écarts annuels de température, et la productivité de la forêt y est largement restreinte par le froid. La photosynthèse est un processus limité par les températures froides, qui inhibent les réactions enzymatiques impliquées dans la fixation du carbone (Ensminger et al. 2009). Par temps froid, l'énergie lumineuse absorbée par les photosystèmes des conifères ne peut être utilisée pour alimenter le transport d'électrons et la fixation du carbone, et est dissipée sous forme de chaleur (Ensminger et al. 2009; Taiz and Zeiger 2006). Ce transfert d'énergie est rendu possible par la réorganisation des pigments chloroplastiques et prévient les dommages causés par la lumière en excès (Ensminger et al. 2009; Taiz and Zeiger 2006). Le photosystème II (PSII) est également inactivé par la détérioration des pigments de

chlorophylle (Ensminger et al. 2009). Ces modifications au niveau du chloroplaste sont généralement accompagnées d'un endurcissement au froid de l'arbre (Ensminger et al. 2009). Ces processus physiologiques sont initiés suivant les premiers épisodes de gel par temps ensoleillé, et largement contrôlés par la température de l'air et la photopériode (Ensminger et al. 2009). Chez les feuillus, la capacité photosynthétique des feuilles est perdue principalement en réponse au déclin de la photopériode (Keskitalo et al. 2005). Les chloroplastes sont entièrement dégradés et les nutriments qui les composent sont relocalisés pour être conservés par l'arbre avant l'abscission des feuilles (Keskitalo et al. 2005). La photosynthèse chez les conifères et les feuillus est donc interrompue durant les mois d'hiver avant d'être reprise au printemps (Körner 2003).

Chez les conifères, la photosynthèse est reprise au printemps en réponse au réchauffement de l'air (Bergh and Linder 1999; Mäkelä et al. 2004; Tanja et al. 2003), et peut être très rapide puisque les constituants de l'appareil photosynthétique sont retenus sur l'arbre pendant l'hiver. L'appareil photosynthétique est réassemblé et restructuré, et la proportion de l'énergie lumineuse qui est utilisée dans les processus photochimiques augmente (Ensminger et al. 2009). Cette reprise peut toutefois être ralentie ou même renversée par l'occurrence de gels intermittents (DeLucia and Smith 1987; Ensminger et al. 2004). Ensminger et al. (2004) ont démontré que des épisodes de gel intermittents renversaient la réorganisation de l'appareil photosynthétique chez le pin sylvestre (*Pinus sylvestris* L.), et DeLucia et Smith (1987) ont mesuré des réductions irréversibles de photosynthèse de 25 à 35% chez des épinettes d'Engelmann ayant été exposées à des températures nocturnes de -5ºC en début d'été. Cette même étude a révélé qu'après l'arrêt d'épisodes de gel printaniers, la température du sol était le principal facteur limitant la reprise de la photosynthèse. Plusieurs auteurs ont également observé une reprise printanière de photosynthèse réfrénée en sol froid, et ont attribué ce phénomène à un ou plusieurs des facteurs suivants : une conductance stomatique réduite, un apport en eau et en nutriments réduit, une production d'hormones réduite au niveau des racines, ou l'altération des dynamiques source-puits d'hydrates de carbone de l'arbre (Bergh and Linder 1999; DeLucia and Smith 1987; Ensminger et al. 2008; Ensminger et al. 2004; Repo et al.

2007; Strand et al. 2002). Chez les feuillus, la reprise printanière de la photosynthèse est conditionnelle à la feuillaison de l'arbre, qui est déclenchée et contrôlée principalement par le réchauffement de l'air (Cannell and Smith 1986). Suite au débourrement, la capacité photosynthétique de l'arbre augmente proportionnellement avec l'aire des feuilles (Kozlowski and Pallardy 1996). Comme chez les conifères, la température du sol influence le recouvrement de la photosynthèse. Par exemple, Wan *et al.* (1999) ont observé un flux d'eau à travers les racines de semis de peuplier faux-tremble plus bas dans des sols à 5 et 10ºC que dans un sol à 20 ºC. Le flux d'eau des racines était positivement corrélé avec la taille des feuilles, l'aire totale des feuilles, la longueur des pousses et la croissance de nouvelles racines. Le climat printanier a le potentiel de déterminer le taux de photosynthèse pour l'ensemble de la saison de croissance, et donc la productivité annuelle de la forêt.

Chez les feuillus comme chez les conifères, le recouvrement de la photosynthèse peut être suivi sur le terrain avec la technique de fluorescence chlorophyllienne. En principe, l'énergie lumineuse absorbée par les molécules de chlorophylle est soit utilisée pour la photosynthèse, dissipée sous forme de chaleur, ou réémise sous forme de lumière fluorescente (Taïz and Zeiger 2006). En mesurant le rendement de la fluorescence, il est possible de connaître la proportion d'énergie utilisée pour les processus photochimiques, et la proportion dissipée en chaleur (Maxwell and Johnson 2000). Ces informations renseignent sur l'état du PSII, et le degré d'efficacité de l'appareil photosynthétique (Maxwell and Johnson 2000). À l'aide d'un fluoromètre, il est possible de mesurer le rendement de fluorescence minimal (F_o), qui correspond au rendement de fluorescence d'une feuille à la noirceur. À ce paramètre s'ajoute le rendement de fluorescence maximal (F_m), qui correspond au rendement de fluorescence lorsque la proportion de l'énergie lumineuse utilisée pour la photosynthèse est nulle. La différence entre les paramètres F_m et F_o, appelée rendement variable de fluorescence (F_v), permet le calcul du rendement quantique potentiel du PSII (F_v/F_m) (Maxwell and Johnson 2000). Le rendement quantique de la fluorescence ($\Delta F/F_m$) est typiquement représenté graphiquement en fonction des différentes intensités de lumière émises par le fluoromètre au cours d'une mesure. Les courbes de lumière qui en résultent servent au calcul de différents paramètres fournissant

de l'information additionnelle sur l'état de l'appareil photosynthétique. Rascher *et al.* (2000) a proposé l'utilisation de trois paramètres calculés à partir des courbes de lumière : le rendement quantique du PSII sous lumière saturante ($\Delta F/F_{m\,sat}$), la densité photosynthétique du flux de photons à saturation ($PPFD_{sat}$), mesurée en µmol m^{-2}, et le taux maximal de transport d'électron (ETR_{max}), mesuré en µmol $m^{-2}s^{-1}$. Ce dernier paramètre est corrélé de près au taux de fixation de carbone de l'arbre (Ralph and Gademann 2005).

Objectifs et hypothèses

Les objectifs de cette étude sont donc (i) d'examiner la réponse physiologique de l'épinette noire et du peuplier faux-tremble à différentes épaisseurs de mousses et de neige en hiver et au printemps; (ii) de comparer les réponses des deux espèces et prévoir un éventuel changement de composition des peuplements d'épinette noire et de peuplier faux-tremble de la forêt boréale mixte en vue des changements climatiques prévus et (iii) d'inférer les conséquences possibles sur la productivité de la forêt. Nous émettons les hypothèses que (i) un dégel du sol retardé au printemps retardera le moment et réduira le taux de recouvrement de la capacité photosynthétique et du débourrement des arbres, tandis qu'un dégel accéléré devancera le déclenchement de ces processus, (ii) les arbres croissant dans un sol privé de son couvert de mousses bénéficieront des températures de sol plus chaudes et d'un meilleur recyclage des nutriments, alors que ceux recevant une épaisseur additionnelle de mousses se trouveront désavantagés par des températures plus froides et une disponibilité des nutriments décrue, (iv) le peuplier faux-tremble sera davantage affecté par un refroidissement du sol davantage que l'épinette noire, qui est mieux adaptée aux sols plus froids.

CHAPITRE 1

ROOT ZONE TEMPERATURE IN BOREAL SPRING DEPENDS ON THERMAL INSULATION AND CONTROLS PHOTOSYNTHETIC CAPACITY IN *PICEA MARIANA* AND *POPULUS TREMULOIDES*

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1.1 Abstract

We assessed the effects of varying moss and snow depths on soil temperature and hence their effects on the physiology of black spruce and trembling aspen in the black spruce-feather moss bioclimatic zone of Quebec, Canada. For one year, ten year-old spruce and aspen were grown with either additional moss cover, removed moss cover, delayed or accelerated soil thawing through snow cover modification or additional N fertilization. Treatments that involved the addition of insulating moss or snow yielded lower soil temperature, while removing moss and snow had a warming effect. A major trend was that soil cover, whether it be moss or snow, increased the rate of photosynthetic recovery in the spring. Moss and snow removal, on the other hand, had the opposite effect and caused lower photosynthetic rates, especially in spruce, with maximal electron transport rate (ETR_{max}) 39.5% lower after moss was removed than with additional moss, and 16.3% lower with accelerated thawing than with delayed thawing. Potential quantum yield of PSII (F_v/F_m) was 3.3% lower without moss than with additional moss, and 3.8% lower with accelerated thawing than with delayed thawing. Impaired photosynthetic recovery in the absence of insulating moss or snow covers were mainly attributed to reduced nutrient assimilation, possibly due to changes in the soil microbiology caused by higher variations in soil temperature. Both species were affected in that way, but trembling aspen generally reacted less strongly to all treatments. Black spruce showed the most differences between treatments, probably because of the shallow organisation of its root system in the soil profile, making mycorrhizal-dependent nutrient assimilation more sensitive to temperature extremes.

Keywords : *Picea mariana*, *Populus tremuloides*, climate change, snow cover, moss cover, soil temperature, photosynthesis, chlorophyll fluorescence, quantum yield, electron transport rate, stable isotopes.

1.1 Introduction

The IPCC fourth assessment report predicts that climate warming in the boreal domain is likely to exceed the global mean warming in other world areas (Christensen et al. 2007). Changes averaged over 21 climatic models project an increase in winter temperature of 5 to 7ºC for western Quebec, Canada (Christensen et al. 2007). This warming could be accompanied by 10 to 25% more precipitation relative to actual conditions (Christensen et al. 2007). Recent climate simulations suggest that this increase in precipitations will not be sufficient to compensate for the increased evapotranspiration caused by higher temperatures, limiting moisture availability (Girardin and Mudelsee 2008). These dryer conditions, coupled with an increase in forest fire activity, could limit moss accumulation on the forest floor (Fenton et al. 2005). Conversely, if the level of precipitations was to excess that of evapotranspiration, moss colonization could be favoured. Another direct consequence of climate warming could include delayed beginning of the snow season in autumn, and accelerated soil thawing in the spring, which would shorten the snow season and increase soil frost occurrence and severity in the autumn and spring (Campbell et al. 2005).

Mosses and snow are important insulators of soils in the boreal domain. Mosses prevent heat gain to the soil by absorbing incoming solar energy and using it for photosynthesis (Miller et al. 1980). Given their lower thermal conductivity compared to soil, mosses create a physical barrier further preventing soil warming (Hinzman et al. 1991). Snow, having a low thermal conductivity, prevents soil freezing in winter, and large temperature variations in autumn and spring. Mosses and snow covers on the forest floor are susceptible to change rapidly with a climatic warming given their direct dependence to climatic conditions (Campbell et al. 2005; Gornall et al. 2007). For that reason, their potential to influence tree growth requires better understanding.

In the boreal domain, forest productivity is largely constrained by low air and soil temperatures. In autumn, photosynthesis in conifers and deciduous trees is down-regulated after the first daytime frosts (Ensminger et al. 2009) and essentially shut down in winter

(Kozlowski and Pallardy 1996). In the spring, photosynthesis is resumed in response to increasing air temperature (Bergh and Linder 1999; Mäkelä et al. 2004; Tanja et al. 2003) and its recovery is largely controlled by intermittent frosts (Ensminger et al. 2008). The transition from winter to spring is a decisive period controlling the annual photosynthetic production, and thus forest productivity. In the spring, soil temperature plays a major role in the recovery of photosynthesis, which is restricted by soil frost and low root-zone temperature (Bergh and Linder 1999; DeLucia and Smith 1987; Ensminger et al. 2008). Soil frost prevents water uptake by roots by increasing the viscosity of water and decreasing the permeability of roots (Kramer 1983). In addition, cold soil inhibits the metabolism and growth of roots, which in turn reduces root water flow (Kozlowski et al. 1991). In conifers, water deficit in needles may occur during spring when high air temperature increases the evaporative demand of leaves and frozen soil prevents water uptake (Berg and Chapin 1994). The influences of the timing of air and soil warming on the recovery of photosynthesis and thus forest productivity are still poorly understood, and the effects of a possible climate change are still uncertain.

Several studies have investigated the response of boreal tree species to varying soil temperature (Bergh and Linder 1999; Domisch et al. 2001; Domisch et al. 2002; Ensminger et al. 2008; Repo et al. 2005; Repo et al. 2004; Repo et al. 2007; Strand et al. 2002). These experiments, carried out either in controlled environments of growth chambers or natural conditions of Fenno-Scandinavian forests, have provided valuable knowledge on the physiological response of European boreal species to soil temperature. All have reported inhibitory effects of cold soil temperatures on the spring recovery of photosynthesis or on phenological events such as budburst. Yet, few experiments have investigated the effects of soil temperature on Canadian boreal tree species (but see Dang and Cheng 2004; Peng and Dang 2003) in Quebec's forest, which presents different environmental conditions such as greater temperature extremes between summer and winter, a thicker snow cover in winter, or the presence of a thick moss cover on the forest floor. In these ecosystems, root-zone temperature might be controlled to a greater extent by mosses and snow, and, therefore, have a greater impact on tree physiological processes. We thus controlled soil temperature

in the field through mosses and snow manipulation and monitored the physiological response of two of the most ecologically and economically important tree species of the Canadian boreal forest, black spruce (*Picea mariana* (Mill.) B.S.P.) and trembling aspen (*Populus tremuloides* Michx.). Black spruce is known for proliferating on cold, poorly-drained soils (Burns and Honkala 1990a) and having a photosynthetic rate more tolerant to cold soil temperatures than trembling aspen (Dang and Cheng 2004), which typically grows on warmer, well-drained soils (Burns and Honkala 1990b). We hypothesized that warmer soil temperature caused by moss removal or snow removal in the spring would particularly favour the spring recovery of trembling aspen, while colder soil temperatures caused by moss addition or snow addition in the spring would impair the recovery of both species.

1.2 Materials and methods

1.2.1 Experimental site

This experiment took place in Quebec's western boreal forest (79º2'W, 49º44'N), within the black spruce-feather moss (*Pleurozium schreberi* (Bird) Mitt.) bioclimatic zone (Doucet and Côté 2009). The experimental setting was established in a 10 year-old black spruce dominated stand that was naturally regenerated after a stand replacing forest fire in 1997. The soil type in the study area is a clay classified as gleysol (Soil Classification Working Group 1998). These clay soils are typical of the area which belongs to the clay belt of Québec and Ontario, and are prone to paludification. The site is covered with a continuous feather- and sphagnum moss ground cover which is underlied by a raw humus layer approximately 20 cm thick. The area has a mean annual temperature of 1.2ºC with the highest (16.1 ºC) and lowest (-18.8 ºC) mean monthly temperatures in July and January, respectively. Mean annual precipitations is 910 mm, with 222 mm occurring as snow (Environment Canada 2008a).

1.2.2 Biological Material and Treatments

The 42 spruces and 42 aspens used for this study were selected in an area of approximately 20 ha, according to their size (from 1.2 to 2.5 m of height) and general appearance (no disease or damage). The stand density was typical of a post fire stand with

sparse saplings and no canopy trees. The experiment was done as a blocked randomized experiment with seven blocks. Within each block, each selected sapling of each species was randomly assigned to one of six treatments (table 1.1): control (C), nitrogen addition (F), moss addition (M+), moss removal (M-), delayed soil thawing (S+) and accelerated soil thawing (S-), in a way that the treatments were homogeneously distributed over the area. In the C treatment, the snow and moss covers were kept intact and no fertilizer was added. The treatment F consisted of the application of the equivalent of 140 kg/ha slow release N fertilizer on a 2.0 m radius around the saplings, and was intended to facilitate differentiation between temperature and nutrition effects in other treatments. In the M+ treatment, the objective was to create lower soil temperatures in the summer, and a sphagnum moss layer approximately 15.0 cm thick was added in September 2007 to cover a 1.5 m radius area around the saplings. At the same time, all moss was manually removed on a 1.5 m radius around the saplings assigned to treatment M-, to raise soil temperature during the summer of 2008. In the S+ treatment, where the objective was to keep the soil at lower temperatures during spring, the snow was shovelled in February 2008, allowing the soil to freeze deeply. In April 2008, the ground was insulated with a layer of hay 15.0 cm thick, and covered with an additional 60.0 cm of snow. The hay was kept in place until mid-July 2008. Treatment S- was meant to create higher soil temperatures in the spring and consisted of shovelling the snow in April 2008 to accelerate soil thawing.

1.2.3 Climatic data and soil temperature measurements

Climatic and soil temperature measurements were recorded from September 2007 to October 2008 (Figure 1.1). Soil temperature, at a depth of 10.0 cm, was recorded every 6 hours with data loggers (iButton DS1990, Maxim Electronics, Dallas, Texas, USA) buried in the vicinity of 63 saplings. Hourly air temperature and precipitation were measured with an onsite meteorological station. Other climatic measurements included relative air humidity as well as wind speed and direction (data not shown).

1.2.4 Bud development

From the beginning of bud development in May (in the case of spruce) and June (in the case of aspen), bud development of the leader shoot of a selected branch was visually monitored every second day for each sapling. For spruce, the buds were assigned to one of the six developmental stages described in Numainville and Desponts (2004). Aspens were evaluated according to the *International Phenological Gardens Illustrated Guide* (IPGIG 1966).

1.2.5 Chlorophyll fluorescence

For the determination of photosynthetic capacity throughout the growing season, chlorophyll *a* fluorescence measurements were performed during spring and summer 2008. The spruce saplings were each measured on 20 occasions from early May until mid-August. The measurements on aspen saplings started mid-June following leaf development, were repeated 8 times on each sapling, and lasted until mid-August. The pulse-amplitude-modulated fluorometer PAM-2100 (H. Walz GMHB Effeltrich, Germany) was used for the measurements. In the case of black spruce, the measurements were performed on attached previous-year (2007) needles, always on the same shoot on a given sapling. For trembling aspen, the measurements were always taken on the same leaf. For both species, a saturating light pulse was first applied to a dark-adapted (20 minutes) leaf or to a group of needles, for the determination of the minimal and maximal fluorescence yield (F_o and F_m, respectively). The potential quantum yield of PSII was calculated as the ratio of variable to maximum fluorescence yield (F_v/F_m). The specimens were then exposed, for a period of 6 minutes, to 12 levels of increasing actinic light intensity (0 – 1800 µmol m^{-2}), and the effective quantum yield of PSII ($\Delta F/F_m$) at each level was recorded. To determine the three cardinal points of light response curves, ie. the maximal rate of electron transport (ETR_{max}), the saturating photosynthetic photon flux density ($PPFD_{sat}$) and the effective quantum yield of PS II at $PPFD_{sat}$ ($\Delta F/F_{m\ sat}$), the resulting $\Delta F/F_m$ *versus* PPFD curves were fitted using a single exponential function as in Rascher, Liebig and Lüttge (2000):

$$ETR=ETR_{max}(1-e^{-b\ PPFD})$$

where b is an independent parameter and $PPFD_{sat}$ is attained at 0.9 ETR_{max}. The model was fit using non-linear regression using the NLIN procedure in SAS v. 9.2 (SAS Institute Inc., Cary, NC, USA).

1.2.6 Carbon, nitrogen and oxygen isotope composition

Analyses for the abundance of carbon, nitrogen and oxygen isotope composition were carried out for the detection of sapling water stress (^{13}C and ^{18}O) and estimation of the fraction of N that entered saplings through mycorrhizal association (^{15}N). Shoot samples were collected from all saplings on May 15th, June 24th and August 13th, 2008. After the shoots were oven-dried at 100°C for 48 hours, spruce needles, as well as aspen leaves and buds were detached from their twigs with a scalpel. The needle, leaf and bud material was ground and homogenized with a bead mill, and samples of 0.5 to 1.0 mg were transferred into tin capsules for ^{15}N and ^{13}C analyses or silver capsules for ^{18}O analysis (IVA Analysentechnik, Meerbusch, Germany). The samples were inserted in an elemental analyser (NA 2500; CE Instruments, Milan, Italy) for $\delta^{13}C$, $\delta^{15}N$, total carbon and total N analysis, and in a high temperature conversion/elemental analyser (TC/EA Finnigan MAT GmbH, Bremen, Germany) for $\delta^{18}O$ analysis, both coupled to an isotope ratio mass spectrometer (Delta Plus; Finnigan MAT GmbH, Bremen, Germany). The isotopic values are expressed in delta notation (in ‰ units), relative to the VPDB (Vienna Pee Dee Belemnite) for carbon, N_2 in air for nitrogen, and the VSMOW (Vienna Standard Mean Ocean Water) for oxygen.

1.2.7 Data analyses

For data analysis the data set was divided into four subsets, each representing a distinct phase of the winter-spring transition. During the last weeks of May, the initial recovery of photosynthetic capacity was temporarily inhibited by a cold spell during which temperatures regularly fell below freezing at night. As of the beginning of June, the photosynthetic capacity gradually recovered until it reached a plateau in the third week of June. We therefore identified the phases of *Initial recovery*, *Frost*, *Recovery after frost* and

Full recovery (figure 1.1; table 1.2). The effects of the treatments on F_v/F_m, ETR_{max}, $PPFD_{sat}$ and $\Delta F/F_{m\ sat}$ during each phase were estimated using analysis of variance for repeated measures. The variable *block* was treated as a random variable. Within each phase and for each parameter, the unstructured, compound symmetry, first-order autoregressive, and first-order ante-dependence covariance structures were tested for best fit based on AIC criterion. The analysis was performed using the procedure MIXED in SAS v. 9.2 (SAS Institute Inc., Cary, NC, USA). Means were compared with Tukey's test and differences were considered significant at $P \leq 0.05$.

1.3 Results

1.3.1 Moss treatments

Mean soil temperatures in treatment M- were slightly higher than the control as of the beginning of January 2008, and increased rapidly during snow melt at the end of April (figure 1.2B). Soil in treatment M+ stayed frozen three weeks longer than in treatment M-, and maintained lower temperatures until the end of the summer. From April to July, the amplitude of diurnal temperature variation was greater in treatment M- by 1 ºC compared to treatment M+. During the initial recovery of spruce, saplings from treatment M- showed significantly lower F_v/F_m and ETR_{max} than either control saplings, or saplings from treatment M+ (figure 1.3A, B). This was accompanied by significantly lower %N in saplings from treatment M-, and a higher C/N ratio (figure 1.4A, E). The moss treatments had little effect on photosynthesis during the frost episodes at the end of May. Only F_v/F_m was found to be significantly lower without moss than in the control and saplings with added moss (figure 1.3A). All other fluorescence, isotopic and nutritional parameters were similar to the control (figures 1.3 and 1.4). During their recovery after frost, spruce with moss removed showed significantly lower F_v/F_m, ETR_{max} and $\Delta F/F_{m\ sat}$ than control saplings or saplings with added moss (figure 1.3). During the full recovery of black spruce, saplings from treatment M- showed significantly lower F_v/F_m, ETR_{max}, $\Delta F/F_{m\ sat}$ and $PPFD_{sat}$ values than the control saplings or saplings from treatment M+ (figure 1.3). For instance, F_v/F_m in spruce was 3.3% lower without moss than with additional moss, but was not significantly different in aspen

(figure 1.4A). ETR_{max} was 39.5% lower in spruce without moss than with additional moss, and 16.57% lower in aspen without moss than with additional moss (figure 1.4B). Spruce saplings with moss removed also showed, in August, significantly higher $\delta^{18}O$ values than saplings with added moss (figure 1.5D). Moss removal in aspen caused significantly lower ETR_{max} and $PPFD_{sat}$ (figure 1.4B, C). In August, aspen from treatment M+ showed significantly higher %N than in treatment M- and in the control (figure 1.6E).

1.3.2 Snow treatments

Until snow removal at the end of February 2008, all treatments had retained soil temperatures above the freezing point (figure 1.2B). The bare soil in treatment S+ rapidly cooled, dropping 5.0ºC in one week after the soil was uncovered. The soil in treatment S+ stayed frozen three weeks longer than treatment S-, and remained colder until the end of the summer. From April to July, the amplitude of diurnal variation in soil temperature was higher in the treatment S- than it was in the treatment S+. Largest differences were observed in May, June and July, where the soil in treatment S- varied daily by 1.4 ºC more than in treatment S+ (figure 1.2B). Spruce with accelerated thawing showed significantly lower F_v/F_m during their initial recovery, along with significantly lower $\delta^{15}N$ than in the control and the delayed thawing saplings (figure 1.5C). Significantly lower %N was also recorded in spruce with accelerated thawing compared to the control (figure 1.5A). The snow treatments had no effect on photosynthesis in spruce during the frost episodes at the end of May, and the successive recovery after frost (figure 1.3). At full recovery, spruce from treatment S+ showed significantly higher F_v/F_m, ETR_{max} and $PPFD_{sat}$ than those from treatment S- (figure 1.3A, B and C). For instance, F_v/F_m was 3.8% lower in spruce with accelerated thawing than in spruce with delayed thawing. ETR_{max} was 16.3% lower in spruce with accelerated thawing than in spruce with delayed thawing. Leaves collected at the end of July on spruce from treatment S- showed significantly lower $\delta^{15}N$ values than the control. In trembling aspen, snow treatments had no effect on any of the fluorescence parameters, nor did they affect the isotopic or nutritional content of the leaves. Bud development occurred, however, two days earlier in aspen from treatment S- than in treatment S+.

1.3.3 Nitrogen addition treatment

N addition had only little effect on the photosynthetic capacity of spruce and aspen. All fluorescence parameters were statistically similar to the control with fertilisation, with the exception of $PPFD_{sat}$, which was significantly higher in spruce at full recovery. Fertilization, however, significantly increased the %N in spruce needles in June and August, resulting in lower C/N ratios. Reductions in %N were recorded in aspen leaves in August. Aspen leaves also showed significantly lower C/N ratios in August. N addition had no effect on the foliar isotopic signatures of either species.

1.4 Discussion

Our results provide clear evidence that moss and snow covers act as important regulators of soil conditions and, therefore, of tree physiological activity. Treatments that involved the addition of insulating moss or snow yielded lower soil temperature, while removing moss and snow in the spring had a warming effect. A major trend was that soil cover, whether it be moss or snow, increased the rate of photosynthetic recovery in the spring. Snow and moss removal, on the other hand, had the opposite effect and caused lower photosynthetic capacity. Both species were affected in that way, but black spruce showed the most differences between treatments. Trembling aspen generally reacted less strongly to all treatments.

1.4.1 Effects of moss treatments

Moss addition delayed soil thawing by more than 3 weeks in the spring, and moss removal created warmer soil conditions as of snowmelt and throughout the entire growing season. Delayed soil thawing did not affect the recovery of photosynthesis in spruce, but faster soil warming was associated with slower recoveries of both F_v/F_m and ETR_{max}. These results contrast with previous studies that documented restricted recovery of photosynthesis in cold soil (Bergh and Linder 1999; Strand et al. 2002). For instance, when warming soil with underground heating cables in a Norway spruce (*Picea abies* (L.) H. Karst.) stand, Bergh and Linder (1999) observed higher rates of light-saturated photosynthesis on heated plots. Decreased photosynthetic capacity in cold soil was reported in several growth

chambers experiments (Ensminger et al. 2008; Ensminger et al. 2004; Repo et al. 2005; 2004). Our results thus suggest that a factor other than soil temperature interfered to suppress photosynthetic processes in spruce following the modification of moss cover. Lower foliar N in the spring in spruce without moss cover (figure 1.5E) suggests reduced nutrient uptake, which could have been caused either by reduced water uptake by roots, by reduced nutrient availability in the soil following moss removal or by impaired capacity for nutrient transfer via mycorhizal associations. Because no soil moisture data was collected on individual saplings during this experiment, it is impossible to confirm or infirm the hypothesis of possible soil water deficiency following moss removal. It is, however, unlikely that the saplings were water stressed during spring. The spring and summer of 2008 received higher than normal precipitations (437.0 mm of precipitation from May to August versus 15-year mean annual precipitation of 326.6 mm) (Environment Canada 2008b). Although fine root damage resulting from soil freeze-thaw cycles was reported in the past (Tierney et al. 2001), $\delta^{13}C$ and $\delta^{18}O$ values did not differ from the control in spring (figure 1.5B et D), suggesting the absence of water stress. Impaired water uptake caused by modified soil conditions or root damage caused by moss removal is, therefore, unlikely to explain our results. Instead, low foliar N (figure 1.5E) likely occurred as a result of reduced soil nutrient uptake.

Reduced nutrient uptake by spruce in the spring could be attributed to lowered soil nutrient availability following moss removal. Mosses are known to efficiently intercept and sequester nutrients from precipitations and throughfall, preventing rapid leaching to deeper soil horizons (Oechel and Van Cleve 1986) and therefore acting as nutrient storage. It is also well known that biological N fixation is the primary input of N in boreal ecosystems (Cleveland et al. 1999), and generally believed that N fixation in boreal forests is primarily achieved by N_2-fixing cyanobacteria colonizing *Pleurozium schreberi* dominated moss carpets (DeLuca et al. 2007; 2002). N_2 fixation varies greatly both in space and time, and has been estimated to vary from 0.5 kg N ha^{-1} in early-successional forests to 2 kg N ha^{-1} in mature forests (Zackrisson et al. 2004). On an annual basis, DeLuca *et al.* (2002) suggested that the rate of N fixation peaked in September and was maintained until early-November.

For those reasons, complete removal of the moss layer in September might have, firstly, reduced the nutrient retention capacity of the soil through accelerated leaching in the fall, during spring snowmelt and the wet summer of 2008. Secondly, moss removal probably deprived the soil from an important fraction of the annual N fixation by cyanobacteria. This hypothesis is supported by the generally faster recovery of N fertilized saplings compared to control saplings (figures 1.3 and 1.4).

Reduced nutrient uptake by spruce in the spring could also be attributed to impaired nutrient transfer from mycorrhizal fungi to tree roots. Boreal soils are poor in easily accessible nutrients, and nutrients are taken up by trees primarily via mycorrhizal fungi (Van Der Heijden et al. 2008). Spruce and aspen associate primarily with ectomycorrhizal fungi (Doucet and Côté 2009). These fungi grow extensively immediately underneath the moss layer, with extensive mycelial mats connecting the tree roots to the overlying moss carpets (Carleton and Read 1991). Authors have reported nutrient transfer from *Pleurozium schreberi* shoots to the roots of ectomycorrhizal *Pinus contorta* (Carleton and Read 1991) and black spruce (Chapin III et al. 1987). Complete removal of the moss layer could, therefore, not only deprive the ecosystem from a nitrogen source and reservoir, but also tree roots of an important nutrient supply via mycorrhizal fungi. Nitrogen leaf concentration is generally believed to be correlated with photosynthesis rate through its effects on chlorophyll synthesis, on the activity of Rubisco and other carboxylating enzymes, as well as on stomatal conductance (Kozlowski and Pallardy 1996). In spruce, impaired chlorophyll synthesis would be reflected in lower effective quantum yield, while low carboxylating enzyme and Rubisco activity would manifest as lowered electron transport rate. This tendency manifested as consistently lower ETR_{max} in spruce without moss cover, and highest ETR_{max} in spruce with N fertilization (figure 1.3). In aspen, moss removal did not reduce foliar N concentrations. Foliar N was rather increased with additional moss at the end of the summer (figure 1.6). This late summer N enrichment might have been caused by an additional N release from senescing and decomposing moss shoots, and could explain the higher electron transport rate in aspen with additional moss (figure 1.3).

1.4.2 Effects of snow treatments

The snow cover manipulation was also efficient in modifying soil temperature. In natural conditions, soil temperature under the snowpack remained close to the freezing point during the winter, and bare soil temperature took only a week to drop to -7.0ºC in February. In spring, additional snow and insulation prolonged the period of frozen soil by three weeks. In other snow experiments (Repo et al. 2007; Strand et al. 2002) carried out in Fenno-Scandinavian forests, soil freezing lasted 6 to 8 weeks longer than in natural conditions. In Eastern Canada, a more rapid transition between winter and summer would accelerate soil thawing. Snow removal in the spring momentarily increased soil temperature during snowmelt, but the subsequent occurrence of a warm spell rapidly covered this warming effect (figure 1.2C). Both spruce and aspen were less responsive to the snow treatments than to the moss treatments. Delayed and accelerated soil thawing in the spring still had physiological implications for both black spruce and trembling aspen, but the variables affected differed in each species. For instance, accelerated soil thawing negatively affected most fluorescence parameters in spruce, but did not influence photosynthesis in trembling aspen (figure 1.4). Instead, aspen was affected phenologically, with accelerated budburst when soil thawing was delayed (table 1.9). As is the case with moss treatments, warmer soil was associated with impaired photosynthetic recovery and reduced foliar N concentrations in spruce, especially in the spring. These results suggest that the modification of snow cover either affected soil N dynamics, or the saplings capacity for nutrient assimilation. Both could be explained by changes in soil biology caused by modified soil temperature regimes in the spring. Snow removal in April 2008 rendered the soil directly exposed to air temperature at a time when night frosts were still frequent. Clein and Schimel (1995) observed that soil microbiology in tundra and taiga soils exposed to freeze-thaw cycles was more sensitive than to differences in temperatures in continuously frozen soil. A single freeze-thaw cycle killed 50% of soil microbial populations, and more than three cycles reduced the ability of microbial communities to decompose soil organic matter and mineralize N (Schimel and Clein 1996). This could explain the lower foliar N concentrations in spruce without snow cover in the spring. Mycorrizal fungi, by associating with the shallow

root system of spruce, become susceptible to greater extremes of temperature. Although mycorrhizal activity is known to persist in frozen soils, repeated freeze-thaw action may physically damage mycelia and reduce their capacity for nutrient transfer (Tibbett and Cairney 2007). This hypothesis is supported by lower $\delta^{15}N$ values in the leaves of spruce with snow insulation in the spring, which is characteristic of trees with enhanced fungal supply of organic N. While transferring organic nitrogen compounds to the roots of tree hosts, mycorhizal fungi discriminate against ^{15}N, leading to ^{15}N depletion in their host (see review by Hobbie and Hobbie 2008).

Slower photosynthetic recovery in spruce could also result from leaf injury caused by snow removal in April. In spring and winter, snow cover not only insulates soil but protects trees against frost damage, dessication and solar radiation (Körner 2003). In the absence of snow cover, high daytime temperatures during spring favour high evapotranspiration rates from exposed leaves, but cool soil restricts water uptake from the roots (Bergh and Linder 1999; Strand et al. 2002). If the water lost by evapotranspiration cannot be replaced by soil water, water stress may occur, causing embolization of vascular tissue and dessication injury to the leaves (Boyce and Lucero 1999; Repo et al. 2005; Tranquillini 1982). Snow cover in 2008 was quite deep and the base of each sapling (0.3 to 0.8 m) remained buried until April. Tree parts buried underneath the snow cover, which prevents evapotranspiration, likely escaped dessication stress. Snow in our accelerated thawing soil treatment was removed during that crucial period, exposing their shoots and leaves (in the case of spruce) to ambient air. At the same time, saplings in the delayed thawing soil treatment were supplied with additional snow coverage. Snow removal might have enhanced evapotranspiration and caused water stress and leave injury, while snow addition might have prevented such stress until snowmelt was complete. The absence of differentiation in ^{13}C and ^{18}O values, which would have confirmed water stress in the spring, could be partially explained by the high amounts of precipitation in the spring of 2008 (Choi et al. 2005). Accelerated thawing caused significantly lower N concentration in the leaves of spruce in spring (figure 1.5), which could explain the slower recoveries of F_v/F_m, ETR_{max} and $PPFD_{sat}$. The snow treatments had no effect on the photosynthetic capacity of trembling

aspen. The deeper root system of aspen, coupled with a lower dependency on mycorrhizal associations for nutrient uptake (Bauhus and Messier 1999), likely make the species less vulnerable to aboveground temperature variations.

Snow treatments had either no or only minor effects on the bud phenology of the saplings in this study. In spruce, the timing of bud burst was not affected (table 1.8) which is in accordance with previous studies with Scots pine, Norway spruce, silver fir (*Abies amabilis* (Dougl.)), noble fir (*Abies procera* Rehd) and black spruce (Bergh and Linder 1999; Domisch et al. 2001; Repo et al. 2004; Van Cleve et al. 1990). In aspen, accelerated soil thawing hastened the onset of budburst (table 1.9). Although few studies have reported the effects of soil temperature on deciduous species, the response might, as is the case with conifers, depend on the species. Because spring photosynthetic recovery of deciduous trees is conditional to leafing, earlier budburst in the spring might contribute to higher annual photosynthetic production (Richardson et al. 2009). However, early budburst can expose new leaves to a higher risk of frost damage in the spring (Saxe et al. 2001).

1.5 Conclusions

Our results emphasize the importance of soil nutrient assimilation during the spring recovery of photosynthesis, which appears to be more limited by nutrient availability than by soil temperature. Moss appears to play a key role in soil N dynamics for its functions in soil insulation, as well as in nutrient storage and transfer. Snow cover during spring acts not only as a regulator of soil temperature, but might also play an important role in tree protection against desiccation. Earlier snowmelt in the spring could affect black spruce and other evergreen conifers that are more susceptible to desiccation stress in the spring than deciduous trees, which develop their leaves after snowmelt. In the context of a possible shorter snow season, the role of moss as an insulator will become crucial, especially in the spring when reduced snow cover will be insufficient in insulating soil against extreme temperatures. Although trembling aspen was reported to be more sensitive to cold temperatures than black spruce (Dang and Cheng 2004) mycorrhizal-dependent nutrient assimilation could be more sensitive to temperature extremes in black spruce due to the

shallow organisation of its root system in the soil profile. Removing soil insulation adversely affected the spring recovery of both black spruce and trembling aspen, and thus their annual photosynthetic capacity. In the light of our results, a shorter snow season might result in overall losses in forest productivity, which cannot yet be quantified from our data. Increased air temperature in the spring could counteract the adverse effects of reduced soil insulation. Forest productivity will ultimately depend on the balance between air warming and the associated increase in precipitation.

This study was the first to assess the effects of varying moss and snow covers on Canadian boreal tree species by modifying site conditions directly on the field. Previous studies which have similarly investigated the effects of soil conditions on Fenno-Scandinavian species have provided useful knowledge on ecological relationships determining the annual photosynthetic capacity and forest productivity in those boreal forest ecosystems. Our study demonstrates that such relationships might considerably differ in Canada's black spruce-feather moss bioclimatic zone, and present limitations when applied to those systems and species. Future research efforts should, therefore, be directed at gaining additional knowledge on other important boreal species, such as balsam fir (*Abies balsamea* (L.) Mill.) and Jack pine (*Pinus banksinana* Lamb.), and this in the various bioclimatic zones of Canada. In the past, the relationship between soil temperature and tree photosynthetic efficiency was mostly studied in isolation, i.e. in pot or greenhouse experiments. However, data from such experiments, which have overlooked temperature effects on soil microbiology, should be handled with extreme care when extrapolating to possible consequences of a climatic warming on tree photosynthetic efficiency. Our study provides clear evidence that the interactions and feedback mechanisms between soil temperature, microbiology, nutrient dynamics and tree physiology are complex and require better understanding, which will only be gained through more integrated research approaches.

1.6 Notation

C	carbon
ETR	rate of electron transport (μmol $m^{-2}s^{-1}$)
ETR_{max}	maximal rate of electron transport (μmol $m^{-2}s^{-1}$)
F_m	maximum fluorescence yield of a dark-adapted leaf
F_o	minimum fluorescence yield of a dark-adapted leaf
F_v	variable fluorescence yield of a dark-adapted leaf ($F_v=F_m-F_o$)
F_v/F_m	potential quantum yield of PSII
N	nitrogen
P	phosphorus
PPFD	photosynthetic photon flux density (μmol m^{-2})
$PPFD_{sat}$ s	aturating photosynthetic photon flux density (μmol m^{-2})
PSI and PSII	photosystems I and II
$\Delta F/F_m$	effective quantum yield of PSII
$\Delta F/F_{m\ sat}$	effective quantum yield of PS II at saturating PPFD
$\Delta^{13}C$	measure of the ratio of stable isotopes $^{13}C:^{12}C$ (‰)
$\Delta^{15}N$	measure of the ration of stable isotopes $^{15}N:^{14}N$ (‰)
$\Delta^{18}O$	measure of the ratio of stable isotopes $^{18}O:^{16}O$ (‰)

1.7 Acknowledgements

This research was financially supported by the Natural Sciences and Engineering research council of Canada (NSERC), the Chair NSERC-UQAT-UQÀM in sustainable forest management, and the consortium Ouranos. The first author would like to thank Dan Kneeshaw and Igor Drobyshev for comments on the manuscript, Raymond Lanctôt, Kasia Richer-Juraszek and Marie-Noëlle Caron for help in the field and Stéphane Daigle for help with statistical analyses.

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1.9 Figures

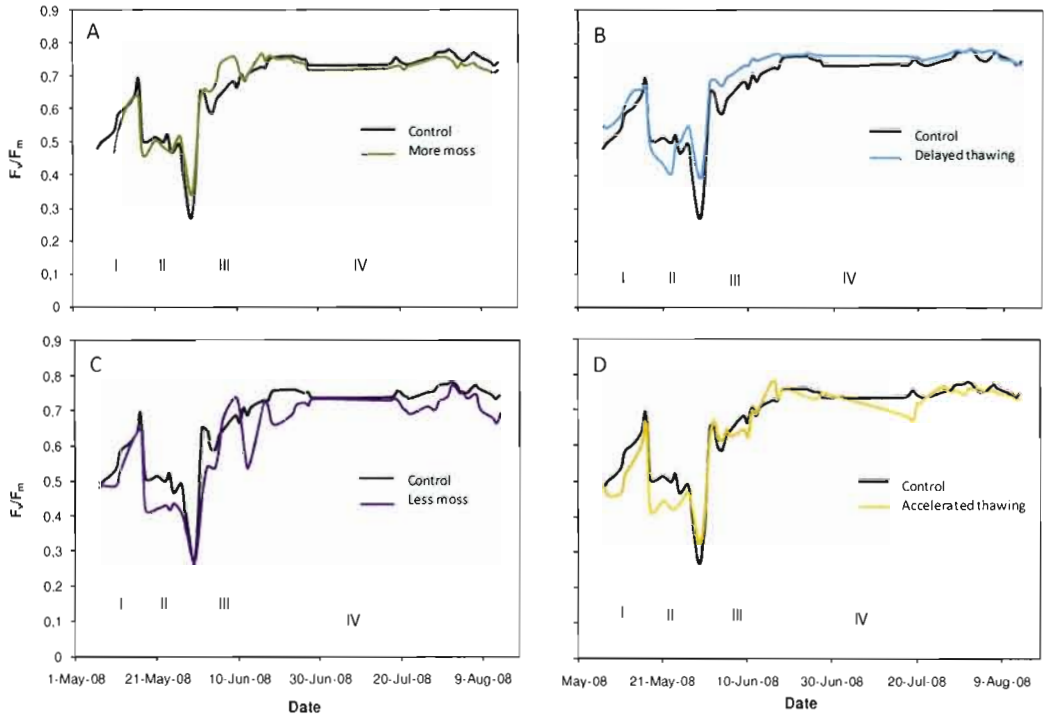

Figure 1.1 Seasonal variations in F_v/F_m in spruce from control and (A) treatment with additional moss (B) treatment with moss removed (C) treatment with delayed thawing and (D) treatment with accelerated thawing. Vertical sections indicate the four phases of photosynthetic development: I (Initial recovery), II (Frost), III (Recovery after frost) and IV (Full recovery).

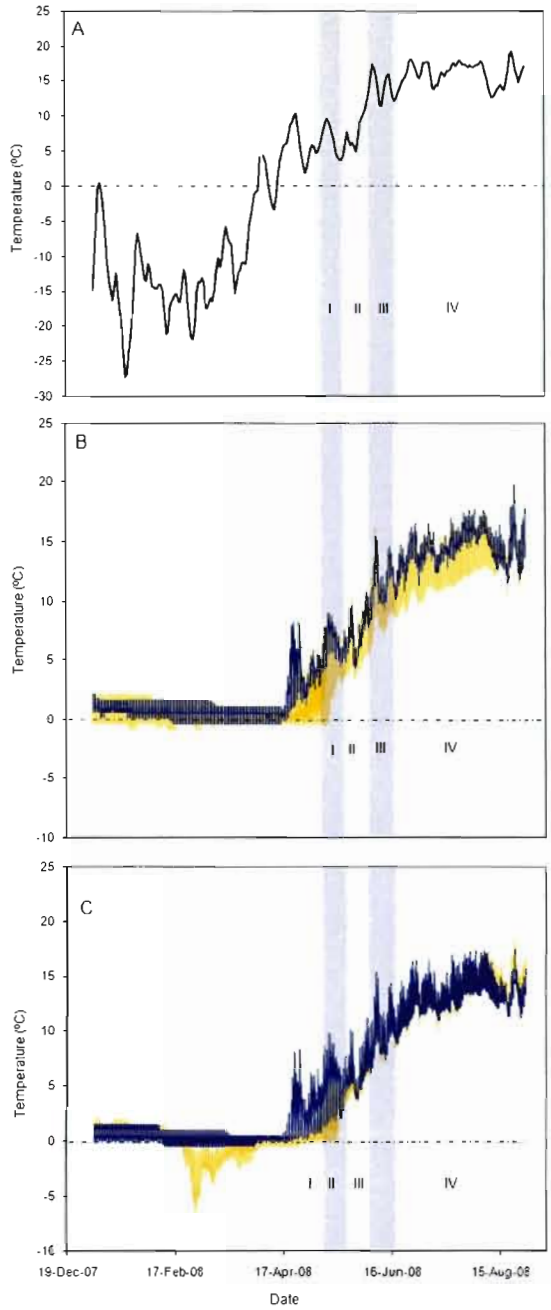

Figure 1.2 Seasonal variations in (A) 5-day running average air temperature, (B) daily soil temperature in the treatment with additional moss (yellow) and in the treatment without moss (blue), and (C) daily soil temperature in the treatment with delayed thawing (yellow), and in the treatment with accelerated thawing (blue). Vertical sections indicate the four phases of photosynthetic development: I (Initial recovery), II (Frost), III (Recovery after frost) and IV (Full recovery).

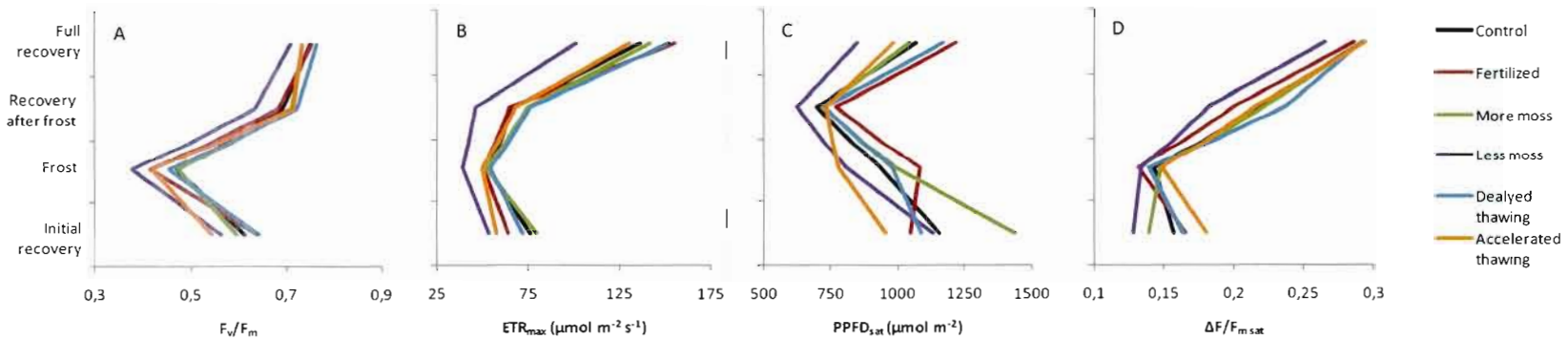

Figure 1.3 (A) Effective quantum yield (F_v/F_m), (B) maximal rate of electron transport (ETR_{max}; µmol $m^{-2}s^{-1}$), (C) saturating photosynthetic photon flux density ($PPFD_{sat}$; µmol m^{-2}) and (D) effective quantum yield of PS II at saturating PPFD ($\Delta F/F_{m\,sat}$) in black spruce needles from control, fertilized, additional moss, removed moss, delayed thawing and accelerated thawing treatments during initial recovery, a frost episode, recovery after frost and full recovery.

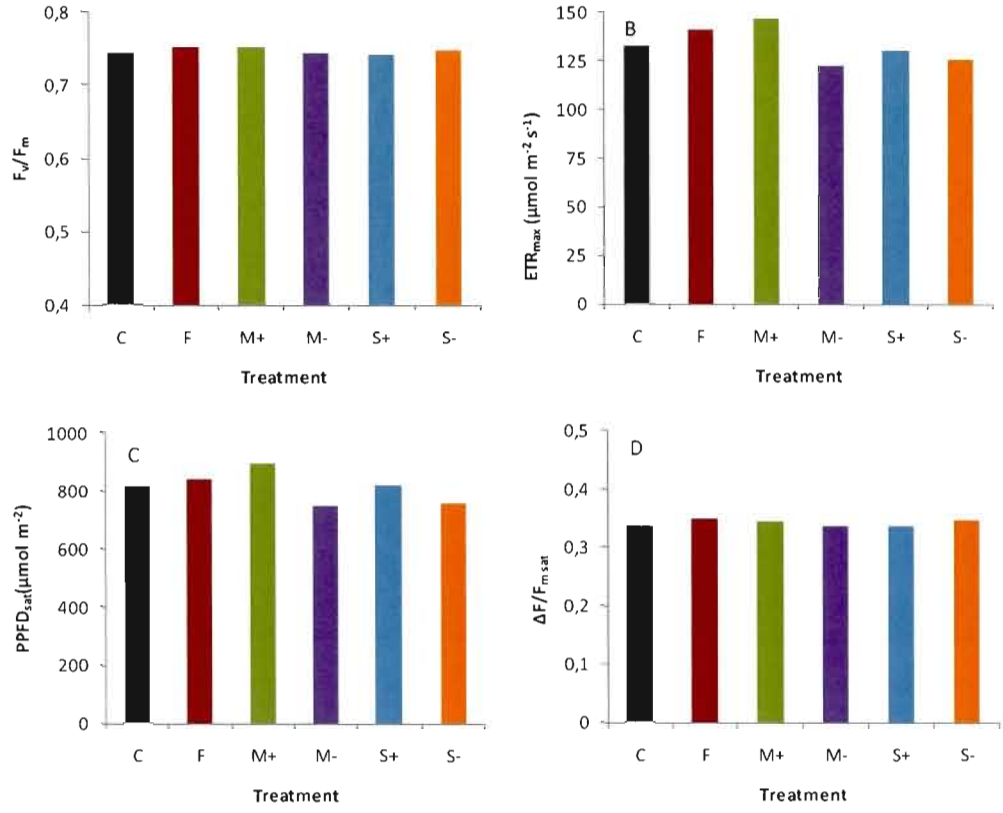

Figure 1.4 (A) Effective quantum yield (F_v/F_m), (B) maximal rate of electron transport (ETR_{max}; µmol $m^{-2}s^{-1}$), (C) saturating photosynthetic photon flux density ($PPFD_{sat}$; µmol m^{-2}) and (D) effective quantum yield of PS II at saturating PPFD ($\Delta F/F_{m\,sat}$) in trembling aspen leaves from control, fertilized, additional moss, removed moss, delayed thawing and accelerated thawing treatments.

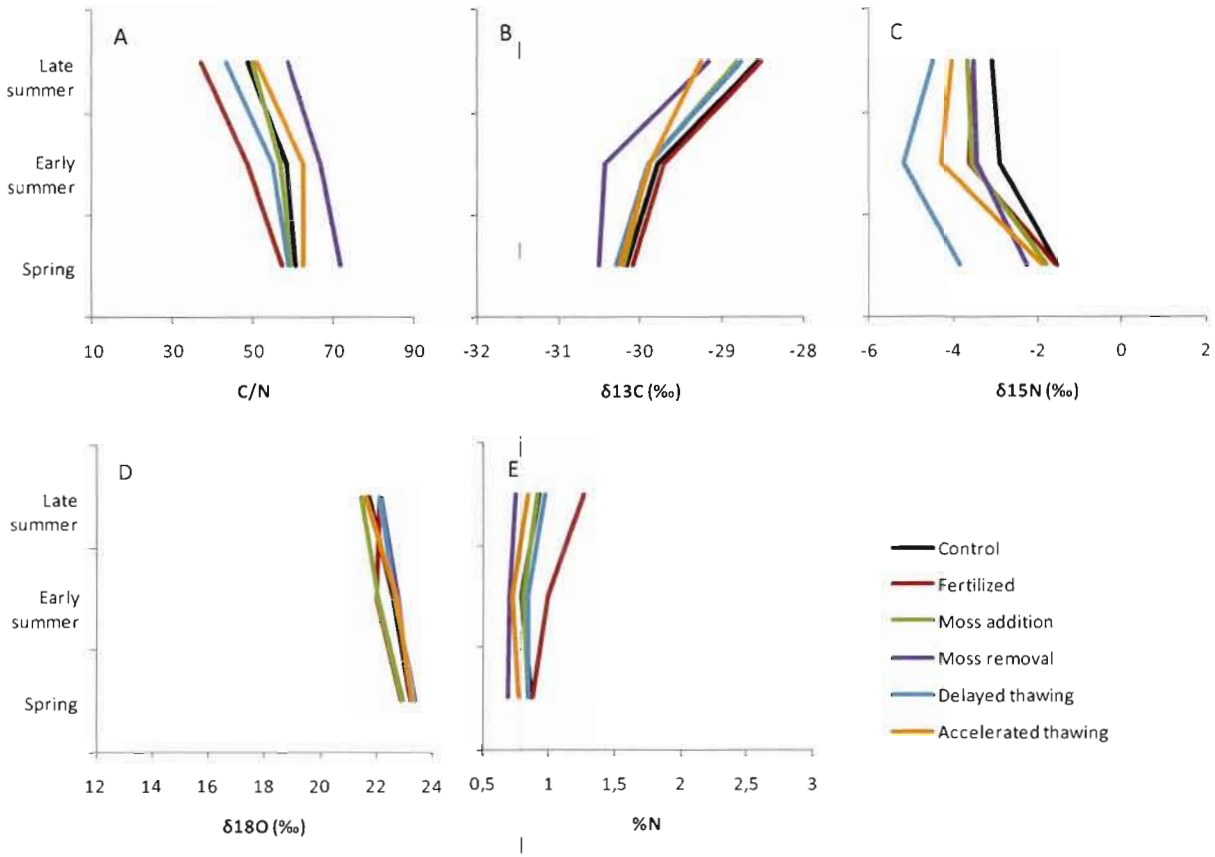

Figure 1.5 Carbon to nitrogen ratios (C/N), $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) and $\delta^{18}O$ (‰) in total foliar organic matter and abundance of N relative to the dry weight of black spruce needles from control, fertilized, additional moss, moss removed, delayed thawing and accelerated thawing treatments during the spring (May 12th), early summer (June 23rd) and late summer (August 13th).

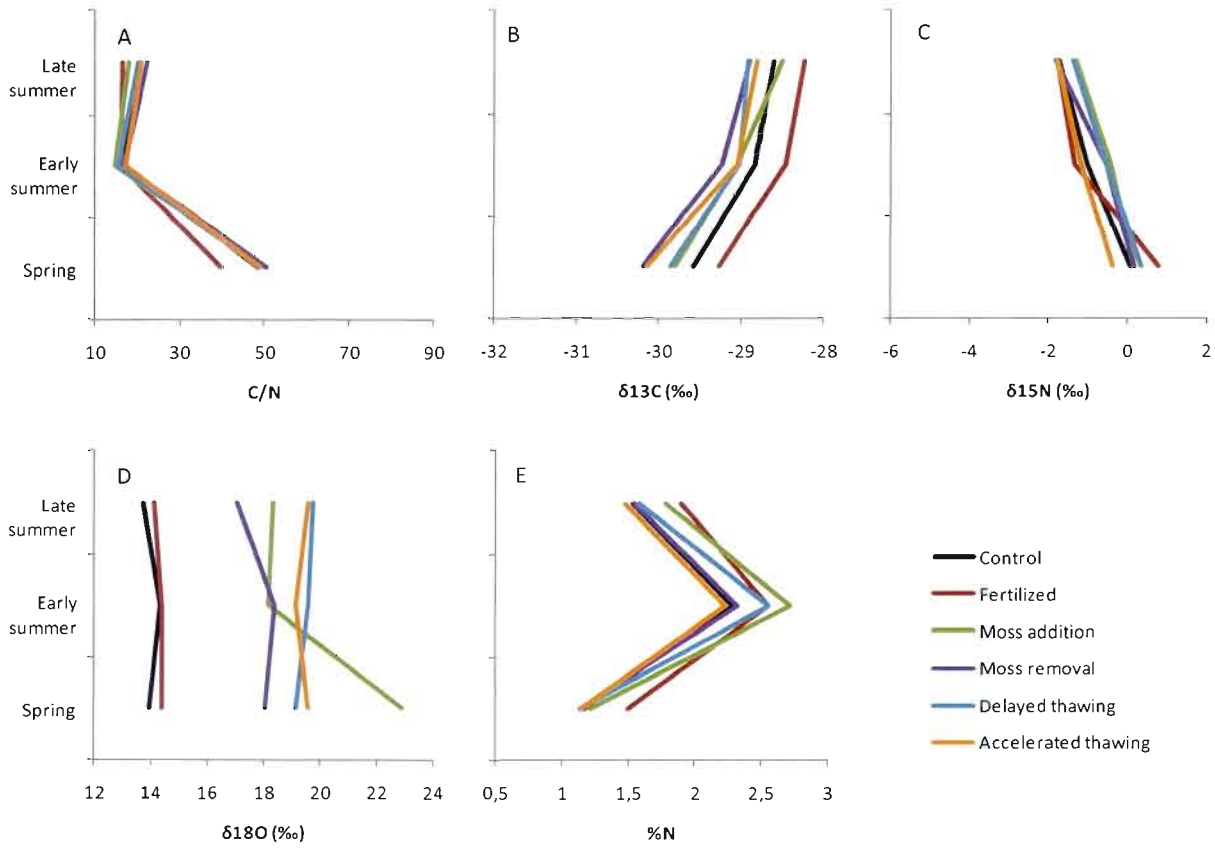

Figure 1.6 Carbon to nitrogen ratios (C/N), $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) and $\delta^{18}O$ (‰) in total foliar organic matter and abundance of N relative to the dry weight of trembling aspen buds and leaves from control, fertilized, additional moss, moss removed, delayed thawing and accelerated thawing treatments during the spring (May 12th), early summer (June 23rd) and late summer (August 13th).

1.10 Tables

Table 1.1 Applied treatments, their abbreviations, summary and timing of manipulations.

Treatment	Abbreviation	Summary of manipulations	Time of manipulations
Control	C	None	–
N addition	F	Application of the equivalent of 140 kg ha^{-1} N fertilizer	May 2008
Moss addition	M+	Addition of a sphagnum moss layer approx. 15 cm thick to cover a 1.5 m radius area around the trees	September 2007
Moss removal	M-	Removal of all moss from a 1.5 m radius area around the trees	September 2007
Delayed thawing	S+	1. Removal of snow from a 2.0 m radius area around the trees	February 2008
		2. Addition of a hay layer approx. 15 cm thick, and of a snow layer approx. 60 cm thick	April 2008
Accelerated thawing	S-	Removal of snow from a 2.0 m radius area around the trees	April 2008

Table 1.2 Stages of photosynthetic recovery for all treatments in spruce, their duration, mean air temperature (ºC) and occurrence of night frosts.

Phase	Recovery stage	Duration	Mean air temperature (ºC)	Night frosts
I	Initial recovery	May 7 - 17	7,5	May 9
II	Frost	May 18 - 30	5,5	May 20, 26, 27, 28, 29, 30
III	Recovery after frost	May 31 - June 17	14	June 4, 12
IV	Full recovery	June 18 - August 13	16	none

Table 1.3 Mean soil temperature per treatment during each stage of photosynthetic recovery.

Phase	Mean soil temperature (ºC)					
	C	F	M+	M-	S+	S-
I	5.1	5.7	4.6	6.3	2.8	5.5
II	5.5	6.2	5.6	6.4	5.0	5.9
III	9.7	10.5	9.8	11.0	9.0	10.3
IV	13.4	14.0	13.6	14.7	13.4	14.0

Table 1.4 Effective quantum yield (F_v/F_m), maximal rate of electron transport (ETR_{max}; µmol $m^{-2}s^{-1}$), saturating photosynthetic photon flux density ($PPFD_{sat}$; µmol m^{-2}) and effective quantum yield of PS II at saturating PPFD ($\Delta F/F_{m\,sat}$) in black spruce needles from control, fertilized, additional moss, moss removed, delayed thawing and accelerated thawing treatments during initial recovery, a frost episode, recovery after frost and full recovery. Means ± SE are shown. Within rows, significant differences between treatments ($P \leq 0.05$) are indicated by different letters.

Phase	Variable	Treatment						F-value	P-value
		C	F	M+	M-	S+	S-		
Initial recovery	F_v/F_m	0.61±0.028 a	0.64 ±0.027 a	0.60 ±0.031ab	0.56 ±0.027 b	0.64 ±0.028 a	0.55 ± 0.027 b	6,1	0,0005
	ETR_{max}	76.2 ±8.4 ab	64.1±8.8 ab	79.9 ±8.8 a	53.8 ±9.4 b	72.0 ±8.8 ab	58.0 ± 10.3 ab	1,31	0,2888
	$PPFD_{sat}$	1155.4 ± 170.3 ab	1049.4 ±164.6 b	1438.5 ± 172.2 a	1129.9 ± 189.8 ab	1086.1 ± 174.7 ab	959.2 ±202.7 b	1,44	0,2409
	$\Delta F/F_{msat}$	0.16 ±0.019 a	0.16 ±0.020 a	0.14 ±0.020 a	0.13 ±0.020 a	0.16 ±0.019 a	0.18 ±0.022 a	0,92	0,4805
Frost	F_v/F_m	0.47 ±0.039 a	0.42 ±0.039 ab	0.47 ±0.039 a	0.38 ±0.039 b	0.45 ±0.039 ab	0.42 ±0.039 ab	1,5	0,2179
	ETR_{max}	53.1±5.8 a	51.1±5.8 a	52.4 ±5.7 a	39.5 ±6.0 a	54.2 ±6.0 a	50.3 ±6.0 a	0,87	0,5128
	$PPFD_{sat}$	939.7 ± 130.7 a	1081.6 ± 128.3 a	996.5 ± 132.3 a	813.9 ± 136.7 a	983.1± 136.3 a	782.4 ± 135.6 a	0,74	0,5998
	$\Delta F/F_{msat}$	0.14 ± 0.016 a	0.13 ±0.016 a	0.15 ±0.016 a	0.13 ±0.017 a	0.14 ±0.017 a	0.15 ±0.016 a	0,24	0,9416
Recovery after frost	F_v/F_m	0.69 ±0.022 a	0.68 ±0.022 ab	0.71± 0.022 a	0.64 ± 0.022 b	0.72 ±0.022 a	0.72 ±0.023 a	3,22	0,019
	ETR_{max}	67.6 ±6.8 a	65.3 ±7.0 ab	75.1±6.7 a	46.5 ±6.8 b	76.2 ±6.8 a	68.4 ±6.8 a	2,69	0,0401
	$PPFD_{sat}$	701.3 ±61.7 a	772.6 ±65.5 a	726.0 ±62.2 a	628.6 ±62.2 a	727.2 ±63.3 a	733.7 ±63.3 a	63,2973	0,7114
	$\Delta F/F_{msat}$	0.22 ±0.010 ab	0.20 ± 0.011bc	0.22 ± 0.011ab	0.18 ± 0.011c	0.24 ± 0.010 a	0.22 ± 0.010 ab	3,64	0,0108
Full recovery	F_v/F_m	0.75 ±0.008 ab	0.75 ± 0.008 ab	0.73 ±0.008 b	0.71±0.008 c	0.76 ±0.008 a	0.73 ±0.008 b	5,65	0,0009
	ETR_{max}	136.5 ±7.2 ab	155.4 ±7.1a	141.7 ±7.2 ab	101.5 ±7.1c	152.0 ± 7.2 a	130.7 ±7.1b	8,65	< 0.0001
	$PPFD_{sat}$	1066.7 ±37.3 b	1218.7 ± 37.3 a	1045.2 ±37.7 b	851.5 ± 37.1c	1170.8 ± 37.9 a	984.8 ±37.0 b	13,61	< 0.0001
	$\Delta F/F_{msat}$	0.2925 ±0.007 a	0.2864 ±0.007 a	0.2922 ± 0.007 a	0.2654 ±0.007 b	0.2919 ±0.007 a	0.2942 ±0.007 a	2,66	0,0418

Table 1.5 Effective quantum yield (F_v/F_m), maximal rate of electron transport (ETR_{max}; µmol $m^{-2}s^{-1}$), saturating photosynthetic photon flux density ($PPFD_{sat}$; µmol m^{-2}) and effective quantum yield of PS II at saturating PPFD ($\Delta F/F_{m\,sat}$) in trembling aspen leaves from control, fertilized, additional moss, moss removed, delayed thawing and accelerated thawing treatments. Means ± SE are shown. Within rows, significant differences between treatments ($P \leq 0.05$) are indicated by different letters.

Variable	Treatment						F-value	P-value
	C	F	M+	M-	S+	S-		
F_v/F_m	0.74 ±0.0055 a	0.75 ±0.0056 a	0.75 ±0.0056 a	0.74 ±0.0055 a	0.74 ±0.0056 a	0.75 ± 0.0056 a	0.82	0.55
ETR_{max}	132.5 ±7.3 ab	141.5 ±7.5 ab	146.8 ±7.3 a	122.5 ±7.2 b	130.6 ±7.5 ab	125.5 ±7.4 ab	1.62	1.18
$PPFD_{sat}$	816.7 ±27.0 bc	844.9 ±27.1ab	894.5 ±27.1a	747.2 ±26.7 c	819.8 ±27.1bc	757.3 ±26.8 c	4.61	0.0031
$\Delta F/F_{msat}$	0.34 ±0.0070 a	0.35 ±0.0072 a	0.34 ±0.0070 a	0.33 ±0.0069 a	0.33 ±0.0072 a	0.35 ±0.0071a	0.88	0.51

Table 1.6 Carbon to nitrogen ratios (C/N), $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) and $\delta^{18}O$ (‰) in total foliar organic matter and abundance of N relative to the dry weight of black spruce needles from control, fertilized, additional moss, moss removed, delayed thawing and accelerated thawing treatments during the spring (May 12th), early summer (June 23rd) and late summer (August 13th). Means ± SE are shown. Within rows, significant differences between treatments ($P \leq 0.05$) are indicated by different letters.

Phase	Variable	Treatment						F-value	P-value
		C	F	M+	M-	S+	S-		
Spring	C/N	60.7 ±3.4 b	57.4 ±3.4 b	59.5 ±3.4 b	71.8 ±3.4 a	58.8 ±3.4 b	62.6 ±3.4 b	3,47	0,014
	^{13}C	−30.1±0.28 a	−30.1±0.28 a	−30.2 ±0.28 a	−30.5 ±0.28 a	−30.3 ±0.28 a	−30.2 ±0.28 a	0,25	0,93
	^{15}N	−1.5 ± 0.84 a	−1.5 ±0.84 a	−1.7 ±0.84 a	−2.3 ±0.84 ab	−3.8 ±0.84 b	−1.9 ±0.84 a	2,11	0,091
	^{18}O	23.2 ±0.33 a	22.9 ±0.33 a	22.9 ±0.33 a	23.2 ±0.33 a	23.4 ±0.33 a	23.3 ±0.33 a	0,55	0,74
	%N	0.87 ±0.040 a	0.88 ±0.040 a	0.84 ±0.040 ab	0.69 ± 0.040 c	0.85 ±0.040 ab	0.77 ±0.040 bc	5,25	0,0014
Early summer	C/N	58.3 ±3.5 ab	48.8 ±3.5 c	56.7 ±3.5 bc	66.8 ±3.5 a	54.9 ±3.5 bc	62.7 ±3.5 ab	3,68	0,010
	^{13}C	−29.8 ±0.26 ab	−29.7 ±0.26 a	−29.9 ±0.26 ab	−30.4 ±0.26 b	−29.9 ±0.26 ab	−29.9 ±0.26 ab	1,06	0,40
	^{15}N	−2.87 ± 0.63 a	−3.62 ±0.63 ab	−3.55 ±0.63 ab	−3.43 ±0.63 ab	−5.17 ±0.63 c	−4.27 ±0.63 bc	2,98	0,027
	^{18}O	22.6 ±0.29 a	22.0 ±0.29 a	22.0 ±0.29 a	22.8 ±0.29 a	22.7 ±0.29 a	22.7 ±0.29 a	1,53	0,21
	%N	0.79 ±0.059 b	1.00 ±0.059 a	0.81±0.059 b	0.70 ±0.059 b	0.84 ±0.059 ab	0.73 ±0.059 b	3,45	0,014
Late summer	C/N	48.7 ±4.2 ab	37.4 ±4.2 c	49.8 ±4.2 ab	59.0 ±4.2 a	43.4 ±4.2 bc	51.2 ±4.2 ab	3,71	0,0098
	^{13}C	−28.5 ±0.34 a	−28.5 ±0.34 a	−28.8 ±0.34 a	−29.2 ±0.34 a	−28.7 ± 0.34 a	−28.7 ±0.34 a	0,99	0,44
	^{15}N	−3.0 ±0.76 a	−3.5 ±0.76 a	−3.7 ±0.76 a	−3.5 ±0.76 a	−4.4 ±0.76 a	−4.0 ±0.76 a	0,88	0,50
	^{18}O	21.7 ± 0.22 ab	22.1±0.22 a	21.5 ± 0.007 b	22.2 ±0.007 a	22.1±0.007 a	21.6 ±0.007 ab	2,39	0,061
	%N	0.93 ±0.065 bc	1.26 ±0.065 a	0.91±0.065 bc	0.75 ±0.065 c	0.97 ±0.065 b	0.84 ±0.065 bc	7,16	0,0002

Table 1.7 Carbon to nitrogen ratios (C/N), $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) and $\delta^{18}O$ (‰) in total foliar organic matter and abundance of N relative to the dry weight of trembling aspen buds and needles from control, fertilized, additional moss, moss removed, delayed thawing and accelerated thawing treatments during the spring (May 12th), early summer (June 23rd) and late summer (August 13th). Means ± SE are shown. Within rows, significant differences between treatments ($P \leq 0.05$) are indicated by different letters.

Phase	Variable	Treatment						F-value	P-value
		C	F	M+	M-	S+	S-		
Spring	C/N	48.9 ± 3.2 ab	40.0 ± 3.2 b	50.2 ± 3.4 a	50.7 ± 3.2 a	49.2 ± 3.2 ab	49.3 ± 3.2 a	1.56	0.20
	^{13}C	−29.6 ± 0.41 a	−29.3 ± 0.41 a	−29.8 ± 0.44 a	−30.2 ± 0.41 a	−29.8 ± 0.41 a	−30.1 ± 0.41 a	0.71	0.62
	^{15}N	0.097 ± 0.65 a	0.80 ± 0.65 a	0.20 ± 0.69 a	0.17 ± 0.65 a	0.35 ± 0.65 a	−0.35 ± 0.65 a	0.44	0.82
	^{18}O	14.0 ± 0.27 a	14.4 ± 0.27 a	13.8 ± 0.29 a	14.4 ± 0.27 a	14.4 ± 0.27 a	14.1 ± 0.27 a	0.98	0.45
	%N	1.16 ± 0.097 b	1.50 ± 0.097 a	1.23 ± 0.10 ab	1.14 ± 0.097 b	1.14 ± 0.097 ab	1.16 ± 0.040 bc	2.06	0.10
Early summer	C/N	16.5 ± 1.0 a	16.0 ± 1.0 a	14.6 ± 1.0 a	16.9 ± 1.0 a	16.5 ± 1.0 a	17.3 ± 1.0 a	1.01	0.43
	^{13}C	−28.8 ± 0.30 a	−28.46 ± 0.30 a	−29.0 ± 0.30 a	−29.2 ± 0.30 a	−29.0 ± 0.30 a	−29.0 ± 0.30 a	0.87	0.52
	^{15}N	−0.97 ± 0.60 a	−1.31 ± 0.60 a	−0.38 ± 0.60 a	−0.52 ± 0.60 a	−0.51 ± 0.60 a	−1.16 ± 0.60 a	0.89	0.50
	^{18}O	18.0 ± 2.1 a	18.4 ± 2.1 a	17.0 ± 2.1 a	22.9 ± 2.1 a	18.1 ± 2.1 a	18.3 ± 2.1 a	1.11	0.38
	%N	2.29 ± 0.19 a	2.56 ± 0.19 a	2.72 ± 0.19 a	2.32 ± 0.19 a	2.56 ± 0.19 a	2.23 ± 0.19 a	1.02	0.42
Late summer	C/N	20.5 ± 2.2 ab	16.5 ± 2.2 c	18.0 ± 2.2 bc	22.2 ± 2.2 a	20.0 ± 2.2 ab	20.9 ± 2.2 ab	4.34	0.004
	^{13}C	−28.6 ± 0.30 a	−28.2 ± 0.30 a	−28.5 ± 0.30 a	−28.9 ± 0.30 a	−28.9 ± 0.30 a	−28.8 ± 0.30 a	0.82	0.54
	^{15}N	−1.69 ± 0.56 a	−1.74 ± 0.56 a	−1.25 ± 0.56 a	−1.78 ± 0.56 a	−1.34 ± 0.56 a	−1.72 ± 0.56 a	0.31	0.90
	^{18}O	18.9 ± 0.54 a	18.4 ± 0.54 a	18.9 ± 0.54 a	18.5 ± 0.54 a	18.9 ± 0.54 a	19.1 ± 0.54 a	0.26	0.93
	%N	1.53 ± 0.090 c	1.90 ± 0.090 a	1.78 ± 0.090 ab	1.55 ± 0.090 c	1.60 ± 0.090 bc	1.47 ± 0.090 c	4.49	0.004

Table 1.8 Mean dates of budburst (bud phases 1, 2, 3, 4, 5 and 6) on a black spruce shoot from control, fertilized, more moss, less moss, delayed thawing and accelerated thawing treatments. Within columns, significant differences between treatments ($P \leq 0.05$) are indicated by different letters.

Treatment	Phase 1	Phase 2	Phase 3	Phase 4	Phase 5	Phase 6
C	May 19 a	June 01 a	June 09 a	June 14 a	June 20 a	June 24 a
F	May 14 a	May 29 a	June 08 a	June 13 a	June 19 a	June 22 a
M+	May 15 a	May 24 a	June 07 a	June 12 a	June 17 a	June 22 a
M-	May 17 a	May 30 a	June 09 a	June 14 a	June 20 a	June 23 a
S+	May 14 a	May 27 a	June 07 a	June 12 a	June 18 a	June 21 a
S-	May 19 a	May 31 a	June 09 a	June 14 a	June 19 a	June 23 a

Table 1.9 Mean dates of budburst (bud phases 1, 2, 3, 4 and 5 on a trembling aspen shoot from control, fertilised, more moss, less moss, delayed thawing and accelerated thawing treatments. Within columns, significant differences between treatments ($P \leq 0.05$) are indicated by different letters.

Treatment	Phase 1	Phase 2	Phase 3	Phase 4	Phase 5
C	June 03 ab	June 07 ab	June 09 ab	June 15 ab	June 19 b
F	June 02 b	June 05 b	June 09 b	June 14 b	June 18 b
M+	June 04 ab	June 07 ab	June 10 ab	June 16 ab	June 21 ab
M-	June 04 ab	June 07 ab	June 09 b	June 15 ab	June 20 ab
S+	June 06 a	June 08 a	June 11 a	June 17 a	June 22 a
S-	June 02 b	June 06 ab	June 08 b	June 14 b	June 19 b

CONCLUSION GÉNÉRALE

Les changements climatiques prévus pour le Québec sont susceptibles de modifier le taux de croissance annuel des arbres. Les mécanismes d'interactions entre le climat, les conditions biologiques et physicochimiques du sol, la physiologie des arbres et la productivité de la forêt sont encore mal compris à plusieurs égards. Pourtant, la croissance de l'épinette noire et du peuplier faux-tremble, deux espèces dominantes de la forêt québécoise, est d'un grand intérêt autant au niveau écologique que commercial. L'objectif principal de cette étude était donc de caractériser la réponse physiologique de ces deux espèces à des changements d'épaisseur de mousses et de neige, deux conditions de site susceptibles de changer rapidement avec les changements climatiques.

Alors qu'un bon nombre d'études similaires ont été réalisées en milieux boréaux fennoscandinaves, cette étude est la première à avoir évalué l'effet de la mousse et de la neige en forêt boréale canadienne, sur des espèces propres à cet écosystème. Notre étude a démontré que les interactions qui dominent en Scandinavie peuvent différer de celles qui dominent en pessière à mousses de l'ouest du Québec. Par exemple, une tendance majeure de nos résultats est la réponse physiologique négative des arbres à l'absence d'une couche isolante au sol, qu'elle soit végétale ou neigeuse, et ce, malgré des températures du sol plus chaudes. Le taux de récupération de la photosynthèse a été réduit par l'absence d'isolation au printemps, et accompagné d'une assimilation d'azote réduite par les arbres. Cette réponse, qui contredit celles observées en Scandinavie sur des espèces comme l'épinette de Norvège ou le pin sylvestre (Bergh and Linder 1999; Repo et al. 2007; Strand et al. 2002) a été attribuée à des perturbations de la microbiologie du sol probablement causées par une plus grande amplitude des variations journalières de la température du sol. Il est probable que les champignons mycorhiziens et/ou organismes décomposeurs du sol en aient été affectés dans leurs fonctions, perturbant les dynamiques de N du sol. Ces résultats suggèrent donc que la relation entre le couvert isolant, la température du sol et la croissance des arbres est moins linéaire que ce qui était préalablement assumé. L'assimilation de nutriments, particulièrement de N, a été un facteur plus limitant que la température du sol dans le recouvrement de la photosynthèse, et l'isolation au sol semble

influencer grandement les dynamiques de N du système. La mousse semble jouer un rôle important pour ses fonctions isolantes, d'entreposage, et de transfert de nutriments. La neige, quant à elle, pourrait non seulement réguler la température du sol au printemps, mais aussi protéger les arbres contre la dessiccation printanière.

Une fonte des neiges plus hâtive au printemps pourrait donc affecter la croissance de l'épinette noire et des autres essences résineuses, qui sont davantage susceptibles à la dessiccation printanière que les essences feuillues, qui ne développent leurs feuilles qu'après la fonte des neiges. Dans le cas d'une saison de neige plus courte, le rôle de la mousse deviendra crucial, particulièrement au printemps et à l'automne, où la neige sera insuffisante pour isoler le sol contre les variations de température de l'air. Malgré qu'il ait été démontré que le peuplier faux-tremble était davantage sensible aux températures du sol froides que l'épinette noire (Dang and Cheng 2004), l'assimilation de nutriments par voie mycorhizienne semble être plus sensible à la température chez l'épinette, qui développe son système racinaire davantage en profondeur dans le profil du sol. L'épinette risquerait d'être plus affectée que le peuplier par une saison de neige plus courte, ou par une réduction du couvert de mousses. À la lumière de nos résultats, les changements d'enneigement prévus pourraient occasionner une baisse de productivité des deux espèces, et affecter particulièrement l'épinette noire. Dans l'éventualité où des conditions climatiques plus chaudes et sèches allaient défavoriser l'établissement de bryophytes sur le sol forestier, les deux espèces pourraient profiter de l'amélioration de la fertilité du sol qui découlerait d'une réduction de la paludification, mais être davantage vulnérables aux variations de la température de l'air à l'automne et au printemps. Réciproquement, un accroissement de l'épaisseur du couvert de mousses favorisait des conditions paludifiées et peu productives (Simard et al. 2007), mais exercerait un effet tampon réduisant l'amplitude des variations de température du sol. Nos résultats ne nous permettent pas de quantifier ces changements de productivité forestière, puisqu'ultimement, celle-ci sera déterminée par l'équilibre entre l'accroissement de la température de l'air et celui des précipitations.

Par le passé, la relation entre la température du sol et la physiologie des arbres a été surtout étudiée en isolation, c'est-à-dire sur des semis poussant en pots ou en serres. Les

relations observées au cours de telles expériences devraient être utilisées avec prudence lorsqu'utilisées pour prédire la réponse de la forêt aux changements climatiques, puisqu'elles ont omis de considérer les interactions entre la température et les processus microbiologiques du sol. Notre étude confirme que les interactions entre la température du sol, l'activité microbiologique, les dynamiques nutritionnelles et la croissance des arbres ne pourront être mieux comprises qu'à travers des initiatives de recherches plus holistiques.

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